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THE INDIAN ZOOLOGICAL MEMOIRS

ON INDIAN ANIMAL TYPES

EDITED BY K. N. BAHL, D.Sc., D.Phil.

III

OSTREA CUCULLATA

(THE BOMBAY OYSTER)

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With 51 Figures in the Text

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EDITOR'S PREFACE

Zoology as a subject in the university curriculum is becoming increasingly popular with the students in India. But there are very few books that deal with the structure and development of common Indian animals. While our students dissect the Indian types, they still use British text-books, which are naturally based on the British fauna. The need, therefore, of books describing our common animal forms is keenly felt in Indian zoological laboratories.

In my Presidential Address to the Zoology Section of the Indian Science Congress at Bangalore (1924), I suggested that a series of memoirs on Indian zoological types should be prepared and published along the lines of the excellent series issued by the Liverpool Marine Biology Committee under the editorship of the late Sir William Herdman.

The proposal has now been taken up by a committee of zoological workers in India, who have decided to issue a series of monographs under the title of "The Indian Zoological Memoirs." The committee have selected the following types for the series and have assigned them to various workers. Memoir I was published in 1926, Memoir II in 1928 and Memoir III is appearing now and it is hoped that others will follow soon.

- I. The earthworm, *Pheretima*, K. N. Bahl, pp. 72, figs. 31. Rs. 1-8.
- II. The shark, *Scoliodon*, Miss E. M. Thillayampalam, pp. 116, figs. 42. Rs. 2-8.
- III. The Bombay oyster, *Ostrea cucullata*, P. R. Awati and H. S. Rai, pp. 107, figs. 51. Rs. 2-8.
- IV. The apple-snail, *Pila*.
- V. The leech, *Hirudinaria*.
- VI. The scorpion, *Palamnæus*.
- VII. The centipede, *Scolopendra*.
- VIII. The prawn, *Palæmon*.
- IX. The fresh-water fish "Rohu," *Labeo*.
- X. The ascidian, *Rhabdocynthia*.
- XI. The starfish, *Pentaceros*.
- XII. The millipede, *Spirostreptus*.

In addition to these, other memoirs on suitable types will be arranged for, as finances permit.

The committee gratefully acknowledge the donation given by the University of Bombay to cover the entire cost of publication of this memoir and offer their cordial thanks to the University.

My best thanks are due to Dr. E. M. Thillayampalam for her kind assistance in editing this memoir.

K. N. BAHL

UNIVERSITY OF LUCKNOW,

January, 1931.

AUTHOR'S PREFACE

There is a great scope for the study of marine animals in the Presidency of Bombay on account of its extensive coast-line along the Arabian Sea. But owing to lack of appreciation of the value of marine zoology, very little work has been done so far. However, the Bombay Government have recently started a Department of Zoology at the Royal Institute of Science and the University of Bombay is also making efforts to provide facilities for research in marine biology and will, it is hoped, establish before long an aquarium for the study of marine animals and plants.

The study of the Bombay oyster was started by us at the Royal Institute of Science about four years ago and the results of our work are embodied in this memoir. Although a great deal has been written on the edible oysters of Europe and other parts of the world, we felt the need of an adequate account of the anatomy and development of the Bombay oyster for the use of students and teachers in India.

We are deeply indebted to Dr. K. N. Bahl, the Editor of the Indian Zoological Memoirs, for his valuable suggestions for the improvement of the manuscript and illustrations, as well as for the trouble he has taken in seeing the memoir through the press.

We are greatly obliged to the Principal of the Royal Institute of Science for the keen interest he has taken in the work and for all the facilities he has provided for research in marine biology. Finally, it is our pleasant duty to acknowledge our indebtedness to the University of Bombay for meeting the cost of publication of this memoir.

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January, 1931.

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INTRODUCTION

The phylum Mollusca to which the genus *Ostrea* belongs includes the true "shell-fish" which are characterised by the possession of an unsegmented bilaterally symmetrical body, a well-developed coelom (gonad and pericardium), a ventral foot as the organ of locomotion, a mantle fold and, in almost all cases, a calcareous shell. Biologically, the Mollusca are a very heterogeneous group and have been classified as follows by Professor Naef¹ in his recent revision of the morphology of the group:

PHYLUM MOLLUSCA

Class I. AMPHINEURA.

Sub-class 1. Solenogastra.

Sub-class 2. Placophora.

Class II. CONCHIFERA.

Sub-class 1. Heteroneura (Prorhipido-glossomorpha).

Order I Gastropoda.

Order II Scaphopoda (Solenconcha).

Order III Bivalvia (Lamellibranchia).

Sub-class 2. Odontomorpha.

Sub-class 3. Cephalopoda.

Class I. AMPHINEURA. The Amphineura are characterised by the possession of a strong cuticle covering the skin, which is impregnated with calcareous spicules or series of plates. The nervous system consists of four apparently equivalent longitudinal cords, the visceral commissure having a post- or supra-rectal position.

Sub-class 1. Solenogastra. This group includes extremely primitive and at the same time degenerate worm-like forms like *Neomenia* and *Chaetoderma*. They are devoid of shell, foot and mantle-fold. The integument is provided with a strongly thickened cuticle impregnated with calcareous spicules or scales. The radula is vestigial. The genital coelom is in open communication with the pericardium and the kidneys serve as

¹ Naef, Adolph.,—"Studien zur generellen Morphologie der Mollusken," Spengel's *Ergebnisse und Fortschritte der Zoologie*, VI, 2, 1926.

genital ducts. The Neomenioidea are monœcious but the Chætodermoidea are dioœcious.

Sub-class 2. **Placophora**. These are bilaterally symmetrical molluscs having a shell composed of eight median plates placed in a longitudinal series. The head-segment is devoid of eyes and feelers. There are numerous pairs of segmentally arranged ctenidia lying in the mantle-furrow. The radula is well-developed but the statocysts are absent. The pericardial cavity has no connection with the gonad but opens into the nephridia. The sexes are separate. The young are hatched as larvæ and pass through a trochosphere stage. Examples: *Chiton*, *Cryptoplax*.

Class II. **CONCHIFERA**. The Conchifera are characterised by the possession of a shell consisting of a *single* plate (calcified from two lateral centres in Bivalvia).

Sub-class 1. **Heteroneura**. This group includes the Gastropoda, the Scaphopoda and the Bivalvia. The posterior metameres in the anal complex are completely reduced; the posterior gills together with their blood-vessels, the kidneys and the pallial ganglia are absent; the visceral loop is so arranged that the visceral commissure lies beneath (or in front of) the rectum in the groove between the body and the roof of the mantle cavity; there is a primary triangular fusion of the pleural, cerebral and pedal ganglia; the heart is pierced by the rectum; the genital products are discharged through the kidneys; the genital coelom is reduced to a mere gonidial sac.

Order I. **Gastropoda**. These are asymmetrical molluscs, a large part of their body being usually twisted up into a spiral and covered with a shell. They have a flat foot by means of which they crawl. A buccal mass and radula are also present.

This group includes forms like snails and slugs, limpets and whelks, and cowries and periwinkles.

Order II. **Scaphopoda**. These molluscs have a tubular shell and mantle. There is a long cylindrical foot trilobed at the extremity. The cerebral and pleural ganglia are fused and the cerebro-pedal connectives are very long. There is a buccal mass with an odontophore. Neither a heart nor eyes are present. The sexes are distinct; the right kidney functions as a gonoduct and the left is purely renal in function.

The Scaphopoda are represented by *Dentalium* and a few closely allied genera.

Order III. Bivalvia.

These are molluscs with a bivalve shell enclosing the whole body; the mantle is divided into a right and a left lobe; the foot is usually wedge-shaped and is adapted to a burrowing habit; there are two lateral and symmetrical gill-plates under the mantle; the cerebral and pleural ganglia are fused together.

All the bivalve forms like the fresh-water mussel, the oyster, *Pecten*, etc. belong to this group.

SUB-CLASS 2. *Odontomorpha*. This class includes a group of ancient cone-shells (e. g. *Hyolithes*, *Conularia*, etc.) which Prof. Naef considers to be a connecting link between the Heteroneura on the one hand and the Cephalopoda on the other.

Sub-class 3. *Cephalopoda*. These molluscs have a distinct head which is surrounded by a circle of sucker-bearing arms representing the front part of the foot; the posterior part of the foot forms a funnel composed of two separate or fused halves. The primitive forms like *Nautilus* still retain an outer shell but in all the higher genera, the shell is internal and is very much reduced. The mantle encloses a large mantle-cavity in which the gills and the nephridial, reproductive and anal apertures are situated. The buccal mass has a radula and two jaws; the ganglia are aggregated together and are protected by an internal cartilaginous skeleton; the genital coelom is continuous with the pericardial cavity; the sexes are separate.

This sub-class contains the largest and the most highly organised forms of all Invertebrates and includes forms like the *Nautilus*, the *Octopus* and the great extinct groups of Ammonites and Belemnites.

The order Bivalvia (*Lamellibranchia*) is classified by Pelseneer¹ on the basis of the structure of the gills as follows:

Gills simple like those of Gastropoda with flat and non-reflected filaments disposed in two rows on opposite sides of the branchial axis; the mantle provided with a hypobranchial gland lying on the outer side of each gill; foot with a plantar surface; large labial palps; two adductor muscles.

Order 1. Protobranchiata.

1. Pelseneer, Paul.—“Mollusca” in Lankester's Treatise on Zoology, London, 1906.

Gills formed of parallel, ventrally directed and reflected filaments; successive filaments being joined together by cilia disposed in "ciliated discs," foot generally provided with a highly developed byssogenous apparatus.

Order 2. Filibranchia.

Gills with branchial filaments united at regular intervals by vascular junctions, reflected ends of filaments being joined to the mantle; edges of the mantle united by one or two sutures; two adductor muscles usually present; gonads with their own proper external orifices.

Order 3. Eulamellibranchia.

Pelseneer divides the order Eulamellibranchia into *nine* sub-orders as follows:

Monomyarian or with a very small anterior adductor muscle, mantle open, foot rather small, gills folded, shell inequivalve.

1. OSTRAEACEA.

Nearly always dimyarian; mantle only slightly closed; gills smooth, shell equivalve with an external ligament.

2. SUBMYTILACEA.

Dimyarian; mantle not extensively closed, with two pallial sutures and two well-developed siphons; gills smooth, foot compressed and elongated; labial palps very large.

3. TELLINACEA.

Two pallial sutures, siphons generally somewhat elongated and partially or wholly united, gills slightly folded, a bulb on the posterior aorta, ligament external.

4. VENERACEA.

Two pallial sutures, short siphons, foot cylindrical more or less elongated, furnished with a byssogenous apparatus; gills much folded; shell equivalve with radiating costae and an external ligament.

5. CARDIACEA.

Dimyarian, extensive pallial sutures and distant pallial orifices, no siphons, foot reduced and without a byssus; shell thick and inequivalve.

6. CHAMACEA.

Mantle closed to a considerable extent; siphons well-developed, gills much folded and frequently prolonged into the branchial siphon; foot compressed and generally byssiferous; shell gaping with a pallial sinus.

7. MYACEA.

Mantle largely closed with siphons, long and united; gills prolonged into the branchial siphon; foot short, truncated, discoid and without a byssus. The shell gaping and devoid

of a ligament, but with a styloid apophysis in the umbonal cavities. 8. ADESMACEA.

Hermaphrodite Eulamellibranchia in which the ovaries and testes are distinct and have separate orifices; foot generally rather small, mantle frequently presents a fourth orifice; external gill-plate directed dorsally and devoid of a reflected lamella; hinge of shell without teeth. 9. ANATINACEA.

The sub-order Ostreaacea is divided into four families:

Synopsis of families

Foot digitiform, with a byssogenous apparatus, borders of the mantle provided with long and numerous tentacles, gills not united with the mantle, shell provided with auriculae.

1. LIMIDAE.

Foot much reduced and devoid of a byssus, heart generally on the ventral side of the rectum, gills fused to the mantle, shell irregular, fixed by the left and larger valve.

2. OSTREIDAE.

Shell thick, inequilateral, the anterior side being the shorter; monomyarian with the muscular impression on a prominent myophorous apophysis.

3. ELIGMIDAE.

Shell elongated, dimyarian, with a very small anterior adductor muscle, shell truncated and gaping posteriorly, foot byssiferous.

The family Ostreidae contains the single genus *OSTREA*, which is defined by Reeve¹ as follows:

Distinguishing characters of the Genus *Ostrea*

Shell bivalve, unimuscular (monomyarian), adhering to stones, shells and roots by the lower valve, very irregular; hinge toothless, with linear margin; ligament partly external, laminated upon a trigonal area in each valve.

This genus contains the following Indian species²:

Synopsis of Indian Species

Shell more or less trigonal, sometimes oblong, extremely hard and plaited, plaits more or less angular, generally small;

1. Reeve's *Conchologia Iconica*. 1871.

2. Although numerous kinds of oyster shells have been collected, it has been very difficult to identify definitely the Indian species of this genus owing to the lack of suitable literature here on the subject. However, a provisional list of the Indian species which can be identified with more or less certainty is given here.

lower valve thick, overlapping the other at the margin, hooded under the hinge margin, hinge elongated, frequently produced at the apex; upper valve flat in the middle, plaited towards the margin; greater portion of the margins of both the upper and lower valves denticulated; muscle scar more or less oblong, striated.

There is so much variation in the shape, size and colour-markings that it is easy to confuse many species with it.

Distribution: It is found along the rocky coasts in the high tide area. It has been collected from rocks round about the islands of Bombay and Salsette.

.. .. . 1. *O. cucullata*, Born.

Shell more or less oblong, solid, with lines of growth, transverse striations well marked, longitudinal fine striations present, plaited (folded), plaits deep and rounded; lower valve larger than the upper with a tendency to grow upwards, with a deep cavity, the latter extending under the hinge margin; ligamental area highly developed, drawn out to a very considerable distance, tapering, with a distinct groove; upper valve flat, opercular in form; dentitions absent; muscle scar more or less oblong.

This species has a superficial resemblance to *O. cucullata*.

Distribution: It is generally found among the clusters of *O. cucullata*. It has been collected from the rocks round about Marmagoa (Portuguese India).

.. .. . 2. *O. cornucopia*, Chemnitz.

Shell irregular, small, seldom exceeding two inches in length; lower valve extensively applied to the rocks, with a deep cavity extending under the hinge line, growing upwards, plaited, plaits radially arranged and deep; margins of the lower valve with characteristic spout-like processes; upper valve small and flat; no denticulations; muscle scar generally dark purple.

Reeve says, "It is difficult to distinguish this species from *O. cucullata*, if indeed they be not identical."

Distribution: It has been found on rocks round about the island of Bombay and Karachi.

.. .. . 3. *O. glomerata*, Gould

Shell very bulky, elongated, oblong, narrow in the anterior region, slightly wider at the posterior end, laminated, lines of growth many; lower valve very thick, especially in the anterior region below the ligamental area; ligamental area drawn out

to a considerable distance, broad, with a deep groove in the middle, the groove generally curving to the left but occasionally to the right, transverse and longitudinal striations in the groove area; upper valve thin, flat and opercular; no denticles on the margin; interior of the valves clear and polished with nacreous surface; muscle scar more or less heart-shaped, glassy opaque.

This species has a superficial resemblance to the figures of *O. rostrata*, Chemnitz, and *O. prismatica*, Gray, drawn in Reeve's *Conchologia Iconica*.

Distribution: It is found in the Bay of Bengal, along the Bombay coast, Goa (Portuguese India), and Dwaraka in the littoral zone.

.. .. . 4. *O. gryphoides*, Newton and Smith.

"Shell very large, compressed, spatulate, rather thick, elongated, foliaceous, with large purplish green scales, lower valve flat; upper convex; hinge broad, ventral margin expanded." Reeve.

Distribution: It is found free from rocks in the littoral zone at Karachi.

.. .. . 5. *O. belcheri*, Sowerby.

Shell flat and of a large size, rounded, foliaceous with conspicuous lines of growth; lower valve slightly concave; ligamental area small; upper valve of the same size and shape as the lower, slightly convex; inner surface of the valves clear and nacreous; no denticulations; muscle scar oblong with a cloudy white or smoky white colour.

Distribution: It is found free from the rocks in the littoral zone along the coast of Bombay.

.. .. . 6. *O. discoidea*, Gould, or *O. rivularis*.
(a Japanese oyster)

Shell small, with undulations, dirty purple in colour, with lines of growth; lower valve flat, thin; upper valve same as the lower but slightly concave; inner surface polished, with big patches of green colour; margins purple or brown; small denticles on the margin near the hinge area; muscle scar circular, large and conspicuous, centrally placed, of a green colour.

Distribution: It is found attached to shells of other oysters near about Karachi.

.. .. . 7. *O. quercina*, Sowerby.
This species may be compared to *O. virginica*. Gmel.

(= *O. canadensis* Lk.) from the East coast of North America. It is, however, of a straighter form and thinner texture and is more foliaceous externally; the left valve is more concave and the inner margins of both valves, as well as the muscular scars, are of deep purplish black colour.

Distribution: Ennur backwater, Madras.

.. .. . 8. *O. madrasensis*, Preston.

In addition to these eight species, the following species of the Indian oyster have been described in the Memoirs and Proceedings of the Manchester Literary and Philosophical Society, Vol. 7, 4th series, but they are not found in our collection:

9. *O. crenulifera*. Sowerby.

Syn. *O. plicata*, Chemnitz.

10. *O. bicolor*. Hanley.

11. *O. lacerata*. Hanley.

BIONOMICS AND DISTRIBUTION

An adult oyster (fig. 1) is a fixed animal always found adhering to some solid object in the shallow waters of the sea. According to Reeve¹, there are about *ninety* species of the oyster distributed all over the world, of which only about *eleven* have so far been described from the coastal waters of India. Of these eleven, *Ostrea cucullata*, the rock oyster, is the most widely distributed species and has, therefore, been selected as the type for this memoir. It has a wide range outside India, being found on the Australian coast and also in Japan, where it has been cultivated for a long time by means of bamboos. It also occurs on the North Island of New Zealand in smaller numbers. It inhabits largely the brackish water area and is found attached in clusters to pieces of rock in the inter-tidal zone; the most suitable places being the mouths of estuaries where there is a constant flow of fresh water. The oyster is attached very firmly to the rock by its left valve; the edges of the shells are very sharp and lacerate the soles of the feet if one walks bare-footed over these rocks.

Crowding of individuals on a small piece of rock is due to prolific production rather than to any gregarious instinct on their part. Young oysters (spat) attach themselves in a short time to any hard object (cultch or collector) near at hand and this leads to a crowding of individuals on all pieces of rock in the vicinity of the mother-oyster, even in artificial cultures. It takes a great deal of time and labour to isolate these oysters for purposes of planting.

Owing to this crowding, the shells of the oyster assume various sizes and shapes which perplex a worker in systematic zoology. The largest left valve, so far collected, measures about 76 by 32 cm., the smallest being 29 by 25 cm. The shapes assumed are triangular, square or oblong with different degrees of concavity of the left valve.

When in water, the oyster opens its valves to a very slight extent so as to allow the water to flow into the mantle-cavity which is divided into the inhalent and exhalent chambers (fig. 5). The water flows into the inhalent chamber and goes out through the exhalent chamber. This current of water supplies

1. Sowerby, G. B.—Reeve's *Conchologia Iconica*, Part IV, 288, 1871.

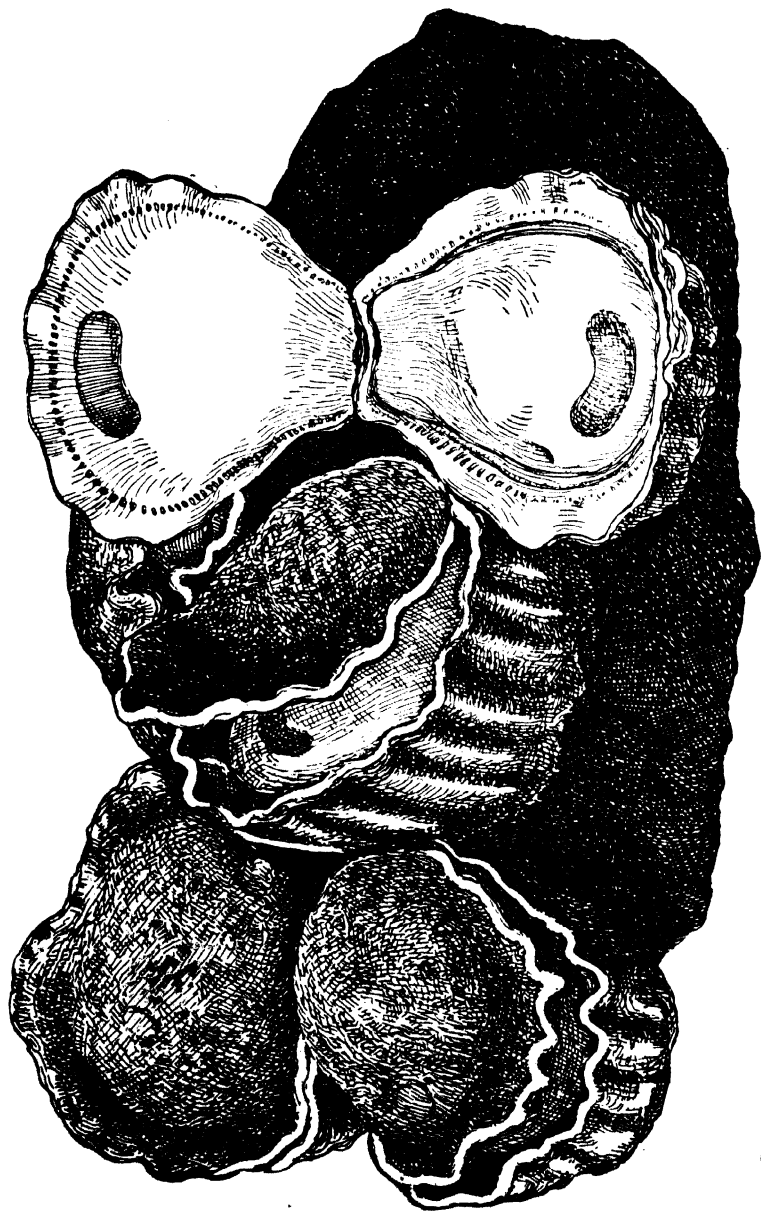


Fig. 1.—The oyster *Ostrea cucullata* *in situ*. Five oysters are seen attached to a piece of rock; one of them with the operculum closed; three with the operculum partially open; the operculum of the specimen on the right side is fully opened to show the position of the adductor muscle, the pallial grooves and ridges, and the hinge. (About two-thirds the natural size).

the animal with food and oxygen. The food of the oyster consists mainly of diatoms, many species of which abound in the coastal waters of the sea. Various species of diatoms are recovered from the intestine of this and other species. Besides diatoms, a few protozoa, mainly ciliates, have also been found in the stomach. It is not definitely known whether these protozoan forms are a part of the diet of the animal or whether they are merely taken in along with the diatoms. Green oysters are found in certain localities in France. The green colour, which has caught the public fancy and has raised the value of these oysters, is really due to the presence of green diatoms in the gills.

The oyster seems to have many enemies in the organic as well as in the inorganic world. Amongst the latter, mud, slime, drifting sand and more than the usual amount of fresh water are the chief enemies. During the monsoon, the mortality amongst oysters due to these causes is very high. During this period, the density of sea water falls below 1.020 by the admixture of a large quantity of fresh water brought into the sea by different rivers and this has an adverse effect on the metabolism of the oyster. Further, these rivers bring down a great amount of mud and silt which are deposited in the intertidal zone where oysters mostly live. Consequently, they are buried beneath the mud and silt and destroyed. Lastly, sand drifts are numerous and dangerous in the monsoon and bury entire beds under them.

Among animals, some enemies attack the early stages, while others are harmful in the adult stages of the oyster. Predatory fishes and crabs break the shells—the former by their teeth and the latter by their claws—and devour the soft parts, especially of the spats. Starfishes and sea-urchins open the shells by a continuous steady pull exerted by their tube-feet. Their stomachs reach out to the soft parts of the bivalves and suck their juices. Boring Gastropods (*Murex* and others) drill holes through the shells with their radulæ and suck in the soft parts of the animal. Sponges like *Cliona*, on the other hand, tunnel through the shells and make them extremely brittle.

Sea-weeds, Hydroids, Barnacles and other sessile animals and plants grow on the surface of the shells. They either make the shell brittle or clog the paths of the water-currents—in either case they are injurious to the animal.

A pea-crab (*Pinnotheres sp.*), a doubtful messmate, sometimes inhabits the oyster. In almost all cases it is the female pea-crab which is found lodged under the gills in the inhalent chamber. The effects of this messmate are seen in the change of colour of the digestive gland, in the stunted growth of the visceral mass and in the change of the sex of the animal. The following table gives an idea of the change of sex.

Sex of animals harbouring pea-crabs.	Numbers examined.	Percentages.
Male ..	71	82·56
Female ..	9	10·46
Hermaphrodite ..	6	6·97
Total ..	86	

The very large proportion of males against females amongst oysters harbouring the pea-crab is remarkable. Ordinarily the proportion of males and females is almost equal, while the existence of the hermaphrodite individuals is almost negligible amongst oysters *without* the pea-crab, as is shown by the following table:

Sex.	Numbers counted.	Percentages.
Male ..	326	41·7
Female ..	445	56·4
Hermaphrodite ..	23	2·9
Total ..	794	

THE SHELL

The shell of *Ostrea cucullata* is inequivalve, the two valves of the shell not being of the same size and shape. The lower valve (fig. 2) is deeply concavo-convex and is permanently attached to a piece of rock, while the upper valve (fig. 3) is flat and forms a sort of lid or *operculum* to the stony case formed by the lower valve. The soft parts of the body are

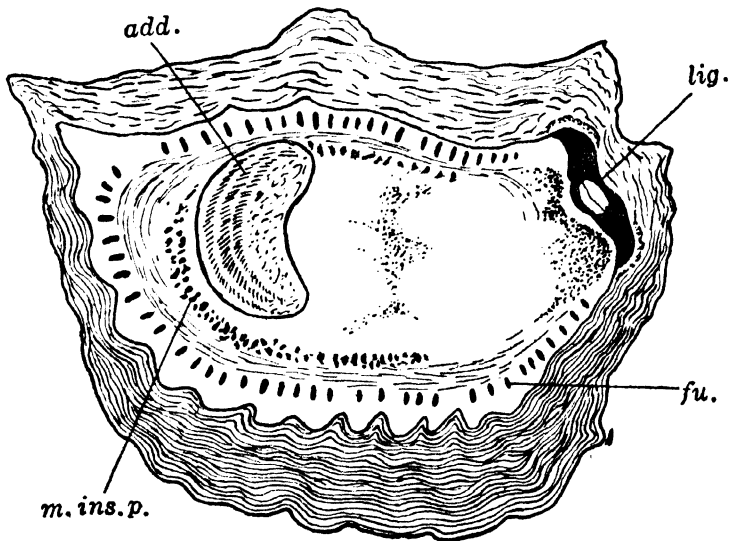


Fig. 2.—The fixed left valve of the shell, inner aspect. *add.*, place of insertion of the adductor muscle; *fu.*, furrows or pits into which the denticles of the right valve fit; *lig.*, hinge-ligament, *m. ins. p.*, places of insertion of the pallial muscles. ($\times$ cir. $1\frac{1}{2}$)

lodged in the deep cavity of the lower valve and are covered by the flat operculum. If an oyster is held sideways with the hinge away from the observer and the flat operculum towards the right hand side, the upper is the dorsal side and the lower the ventral; the posterior end lies towards the observer and the anterior end away from him. Therefore the two valves really represent the right and left sides of the animal and consequently the flat operculum is spoken of as the *right valve* and the large fixed valve as the *left valve*.

In the early stages of development of the oyster, the two valves are of the same shape and size and therefore perfectly symmetrical. The inequivalve condition of the shell is a result of the later growth of the animal. In *Ostrea cucullata*, there is a great variation in the size and shape of the shell, due probably to the close crowding of the individuals of this species.

Externally the shell is rough and stony in appearance with an irregular broken surface and a dirty white or dark brown colour. The colour, however, varies a great deal and various shades of purple, grey or green are met with. A conspicuous streak of a dark purple colour is generally present on the right valve and runs from the hinge-line towards the outer margin. The margins of both valves present a wavy appearance, being produced into folds and grooves, which are radially placed,

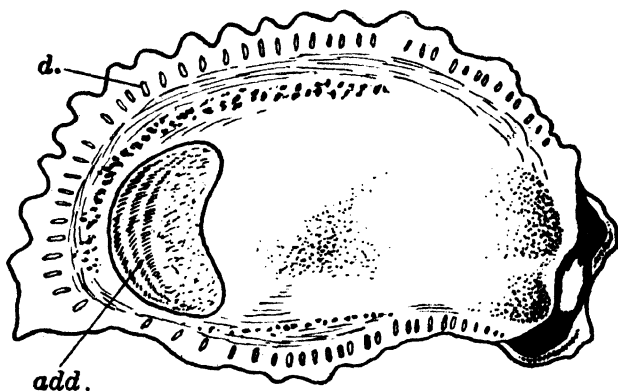


Fig. 3.—Inner aspect of the right valve or the operculum. *add.*, place of insertion of the adductor muscle; *d.*, denticles. ($\times$ cir. $1\frac{1}{2}$.)

closely fitting into one another when the shell is closed. These folds are specially prominent on the left valve, the margin of which has a tendency to grow upwards beyond the edges of the operculum.

The concentric lines of growth found in other Lamellibranchia like *Cardium* are hardly visible in the oyster.

The inner surface of the valves is smooth and shiny and is pearly white in appearance, but occasionally purple or brown patches are seen in places while the margins are invariably purple or black. A big crescent-shaped scar situated excentrically indicates the place of attachment of the single adductor muscle. The scar is generally dark purple in tint but

is sometimes brown and very rarely white. The right valve bears a row of small, close-set denticles placed all round at a short distance internal to the margin (fig. 3). These denticles fit into a series of corresponding furrows on the left valve. Owing to the interlocking of folds and grooves on the margins of the shell on the one hand, and the denticles and furrows within the margin on the other, the shell, when closed, becomes completely water-tight. In this condition the oyster carries on its life-processes with the help of the water enclosed within the shell for the period of its exposure to the atmosphere at the time of the receding tide.

The pallial line, which is a well-marked characteristic of *Cardium* and other Bivalves, is represented only by a series of small depressions lying along a continuous line within the inner margin of the valves, which indicate the line of insertion of the pallial muscles (fig. 2).

The hinge forming the anterior boundary of the animal is smooth and straight, there being no teeth of any kind along the hinge-line. The hinge-ligament (fig. 4) is really an uncalcified part of the shell and is extremely elastic. When the adductor muscle is relaxed, the hinge-ligament pulls the valves of the shell slightly apart so as to enable the animal to keep up the in-going and out-going currents of water.

The shell consists of the three layers—the periostracum, the prismatic and the nacreous layers—as are characteristic of other Bivalves (fig. 7). Of these, the periostracum which is the superficial horny layer is very much thickened in the oyster.

GENERAL ANATOMY

Before examining the different systems of the body in detail, it will be well to know the general arrangement of the soft parts of the body enclosed within the shell.

The best way to start the dissection is to remove the right valve by passing the blade of a knife beneath it and cutting across the adductor muscle without damaging the soft parts, which lie in the cup-shaped left valve. On lifting up the right valve, the body is seen to be covered over by a sheet of soft muscular tissue, the right *mantle-lobe*. During life, this mantle-lobe lines the inner surface of the operculum which is really a cuticular secretion of the mantle. There is a similar mantle-lobe on the left side of the animal lining the inner surface of the left valve. The right and left mantle-lobes enclose a large space, the *mantle-cavity*. On removing the right mantle-lobe, we expose the mantle-cavity and the principal structures lying within it (fig. 4). The gills, the labial palps and the edge of the left mantle-lobe lie on the ventral side, while the adductor muscle, the pericardium, the visceral mass and the rectum lie towards the dorsal side of the animal.

The *mouth* is situated at the extreme anterior end between the labial palps and leads into a long *oesophagus* which in its turn opens into a spacious *stomach* (fig. 6). A large dark brown mass, the *digestive diverticulum*, surrounds the stomach on all sides. The stomach gives off an outgrowth, the *crystalline style sac* and leads into the *intestine* which forms a loop on the left side and is continued into the *rectum* (fig. 5). The rectum runs along the dorsal border of the adductor muscle and ends in the *anus* at the tip of a small papilla. The whole of the alimentary canal, except the rectum, is compactly massed together in the *visceral mass* (figs. 4 and 5), which has to be unravelled in order to display the different parts.

The cephalic region is very rudimentary as in other Bivalves and is represented by a pair of labial palps only, there being no definite prostomial region. In the adult, there is no trace of a foot which is found only in a rudimentary condition in the larval stages. The adult oyster is firmly fixed to a rock or some other hard object and never leaves its place of

attachment. Hence there is no necessity for any organ of locomotion.

The gills form four "demi-branches" or gill-plates, the anterior ends of which are enveloped by the two pairs of labial palps.

The heart is enclosed in the *pericardium* (figs. 4 and 5) between the adductor muscle and the visceral mass and consists of a large muscular ventricle and a pair of thin-walled auricles.

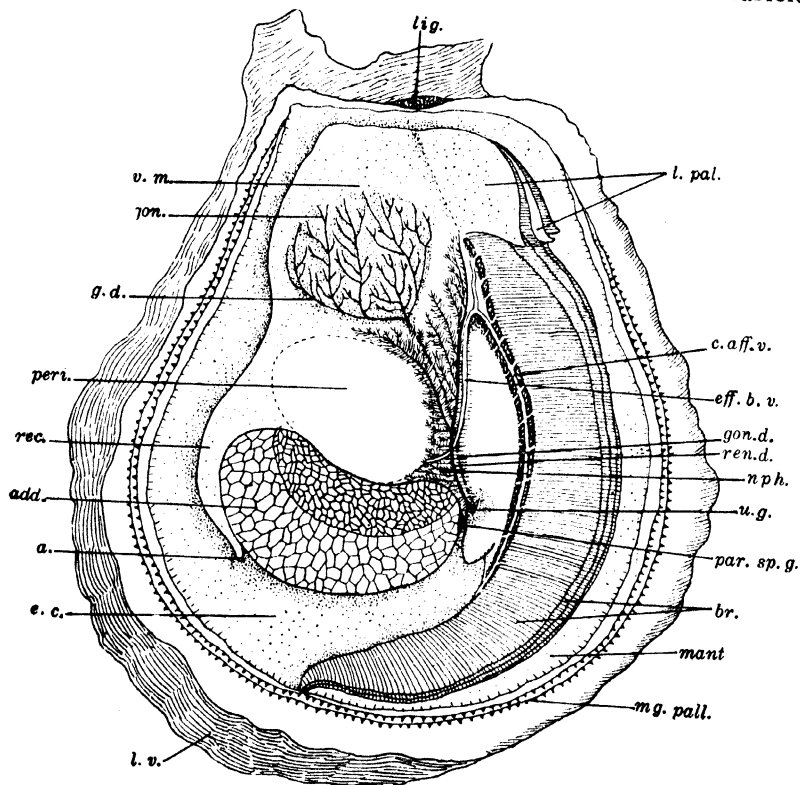


Fig 4.—General anatomy of the oyster as seen on removal of the operculum (right view). *a.*, anus; *add.*, the adductor muscle; *br.*, branchiae or gills; *c. aff. v.*, common afferent vessel; *e. c.*, exhalent or supra-branchial chamber; *eff. b. v.*, efferent branchial vessel; *gon.*, gonad; *g. d.*, gonidial ductules; *gon. d.*, gonidial duct; *lig.*, hinge-ligament; *l. pal.*, labial palps; *l. v.*, left valve; *mant.*, left mantle-lobe; *nth.*, mouth; *mg. pall.*, margin of the pallium or mantle; *nph.*, nephridium; *par. sp. g.*, parieto-splanchnic ganglia; *peri.*, pericardium; *rec.*, rectum; *ren. d.*, renal duct. *u. g.*, urino-genital groove or vestibule; *v. m.*, visceral mass. ($\times$ cir. 2.)

The nervous system is simple. The cerebral ganglia are very small. The parieto-splanchnic ganglion is paired and lies slightly pressed against the ventral surface of the adductor muscle. It sends a pair of conspicuous nerve cords, the branchial nerves, to innervate the gills and also supplies nerves to the adductor muscle and the mantle.

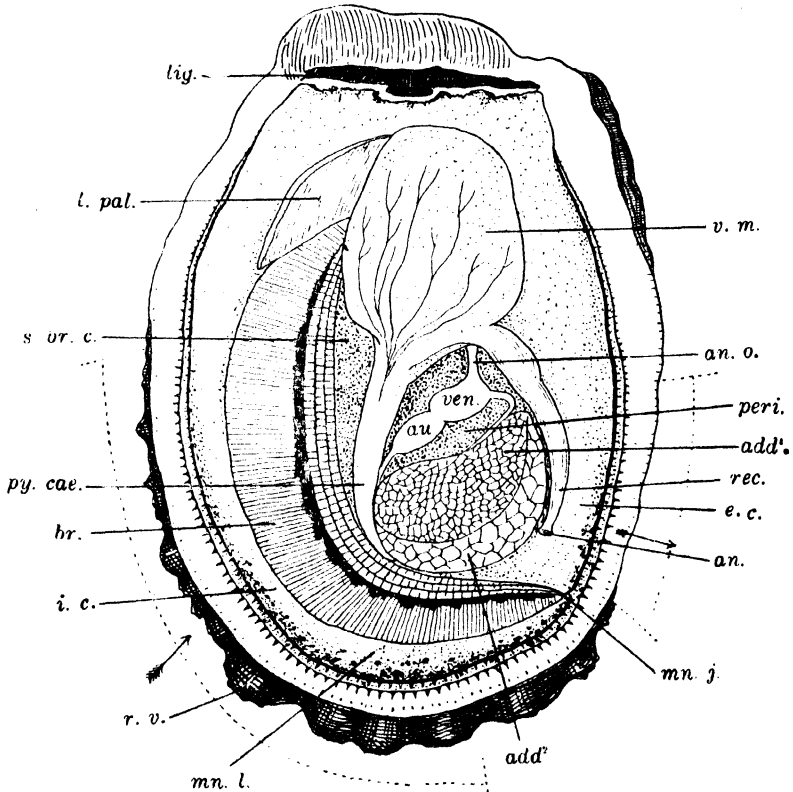


Fig. 5.— General anatomy of the animal as seen from the left side. The dotted line on the left indicates the extent of the inhalent current of water, while the dotted line on the right shows the extent of the exhalent current. *add*¹., the anterior portion of the adductor muscle; *add*²., the posterior portion of the adductor; *an.*, anus; *an. o.*, anterior aorta; *au.*, auricle; *br.*, branchiae or gills; *e. c.*, exhalent chamber; *i. c.*, inhalent chamber; *lig.*, hinge-ligament; *l. pal.*, labial palps; *mn. j.*, junction of the right and left mantle-folds; *mn. l.*, right mantle-lobe; *peri.*, pericardium; *py. cae.*, pyloric caecum; *rec.*, rectum; *r. v.*, right valve or operculum; *s. br. c.*, supra-branchial chamber; *ven.*, ventricle; *v. m.*, visceral mass. The thick black jagged line along the dorsal line of the gills is the line of attachment of the gills with the left mantle-lobe which has been removed. ($\times$ cir. 3.)

The reproductive organs are simple pouches, the walls of which give rise to generative cells. In the breeding season, these organs occupy the whole of the visceral mass. Both the gonads and the renal organs are paired and have separate openings to the exterior.

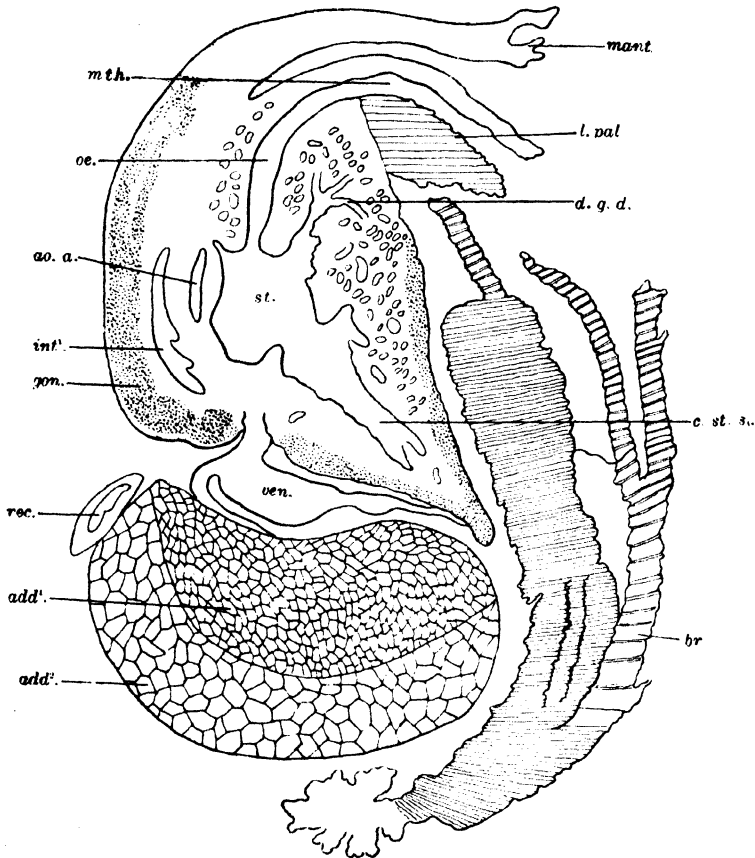


Fig. 6.—A vertical longitudinal section of the oyster, taken a little to the left of the median line, showing the relative position of the different structures of the body. *add¹*, anterior part of the adductor; *add²*, posterior part of the adductor; *ao. a.*, anterior aorta; *br.*, branchiae; *c. st. s.*, crystalline style sac; *d. g. d.*, ducts of the digestive gland; *gon.*, gonad; *int¹*, ascending limb of intestine; *l. pal.*, labial palp; *mant.*, mantle; *mth.*, mouth; *oe.*, oesophagus; *rec.*, rectum; *ven.*, ventricle. ($\times$ cir. 6)

THE PALLIUM OR MANTLE

The *pallium* or *mantle* is an important molluscan organ consisting of two membranous flaps, the *mantle-lobes*, one on each side of the body, enclosing all the essential organs of the animal. The edges of these mantle-flaps are free except at their anterior and posterior ends, where they are fused together to form the so-called "sutures". The anterior suture lies next to the hinge of the shell, while the posterior suture at the hinder end is firmly attached to the posterior termination of the gill-plates. Besides these sutures, both mantle-lobes are united along the middle line of their length with the bases of the outer gill-plates and the visceral mass, thus dividing the enclosed pallial cavity into two chambers—a small dorsal or *exhalent chamber* and a large ventral or *inhalent chamber* (fig. 5). The gills and the labial palps lie in the inhalent chamber while the rectum opens through the anus into the exhalent chamber. On removing the *operculum* in a live animal, a water-current can be seen entering the ventral posterior half of the inhalent chamber and another leaving the exhalent chamber through its posterior dorsal portion (fig. 5).

Each pallial lobe shows three well-marked regions: the proximal, middle and distal or marginal, each distinguished by its structural peculiarities. The proximal region includes the anterior and central portions of the mantle extending on the shell up to the irregular and imperfect pallial line. The greater part of this mantle area is adherent to the underlying visceral mass. In texture, it is soft, thin and transparent, being made up of two parallel layers of epithelial cells enclosing a network of connective tissue between them. The middle region is translucent in appearance and surrounds the proximal region. It contains radial and longitudinal muscles and is extremely contractile. Its outer surface is lined by secretory epithelial cells amongst which are found a few scattered eosinophilous cells (fig. 7), while the inner surface is lined with ciliated epithelium. Between the two epithelial surfaces occur pigment-cells and blood sinuses which are filled with blood and give rigidity to this area. The ciliated epithelium is highly sensitive to touch.

The third or the marginal region is muscular and very much thickened. It is pigmented and is fringed all along its

edge with short sensory tentacles (fig. 5). Further, the free edge is pleated longitudinally into three parallel folds, called the shell-fold, the sensory fold and the velar fold (fig. 7). The outermost is the *shell fold*, which is narrow and lies in contact with the growing edge of the shell-valve. The middle or the *sensory fold* bears simple digitate processes, the tentacles, which are highly contractile and extremely sensitive. The shell-fold and the sensory fold together form the true pallial margin. The innermost pleat, or the *velum*, is broad and projects into the mantle-cavity almost at right angles to the mantle-edge. The velar folds of the two sides come close together in the living animal and form a kind of sieve through which the water-current passes into the mantle cavity.

The mantle being a soft fleshy membrane is kept in a stretched position on its shell-valves: firstly, by the pallial muscles inserted on the shell all along the pallial line, and, secondly, by a cuticular structure, the *periostracum* (fig. 7), inserted on the edge of the mantle in the so-called periostracal groove between the outer secretory and the middle sensory folds. The periostracum holds the edge of the mantle in place and is itself continued over the edge of the shell.

Microscopic structure of the mantle.

Both the inner and outer surfaces of the mantle are lined with a single layer of epithelial cells, the outer epithelium consisting of secretory cells and the inner of ciliated cells. Fig. 7 represents a transverse section of the free edge of the mantle and shows the structure and disposition of the three parallel folds of the marginal region, besides the position of the blood-spaces, the muscles, the pallial nerves, the tentacles, the periostracal groove and the periostracum.

The velum has an inner epithelial covering of tall columnar ciliated cells with mucus glands interspersed amongst them. The core formed of loose connective tissue is traversed by muscle-fibres and contains a few pigment cells. The epithelium of the sensory fold consists of short cubical cells with large rounded nuclei, having a few scattered eosinophilous cells beneath them. A few sensory cells with short cilia and a few mucus-gland-cells are found scattered amongst the ordinary epithelial cells. The underlying connective tissue contains pigment cells as well as numerous radial muscles. Lastly, the secretory fold, which deposits ~~nacre~~ ~~is covered~~

over by an epithelium of large cubical cells with prominent nuclei. The eosinophilous cells are also found in this fold underneath the epithelium. No mucus glands or pigment cells are seen in this fold but muscle fibres are abundant in the connective tissue.

The connective tissue of the mantle is thin and delicate and is full of blood-spaces, especially in the central region. Near the margin, the connective tissue is traversed by the circum-pallial artery and nerve.

Both radial and longitudinal muscles are present, of which the former are best developed. Bundles of muscle-fibres extend into the margin where they branch and are inserted on the valves of the shell along the irregular pallial line. By virtue of these radial muscles, the mantle is contracted away from the margin of the shell while distension is brought about by the turgidity of the mantle—when the blood-sinuses found in it are filled with blood—and by a relaxation of the pallial muscles.

The pigmentation of the mantle is characteristic. The pleated margins of the mantle-lobes and their inner surfaces in most cases are deeply pigmented. The development and the distribution of pigment in this oyster resemble those of the pearl-oyster (*Margaritifera vulgaris*) but differ from those of the window-pane oyster (*Placuna placenta*) in which practically the whole of the internal surface is covered with a black pigment. Hornell¹ and Herdman² believe that continuous exposure to bright sunlight brings about the development of the dark pigment. They have also noticed considerable differences in the degree of pigmentation in oysters of shallow and deep waters. We have observed similar differences in the development of the pigment in *Ostrea cucullata* found in exposed and sheltered places. Oysters found near high-tide level have the black pigment well developed, even on the inner surfaces of the mantle lobes, while those in deep waters, which are seldom exposed to the air, have their pigment diffusely scattered near the margin only. The reason for similar development of the pigment in the pearl oyster (*Margaritifera sp.*) and the rock oyster (*O. cucullata*) is that the shell valves of both are so thick and opaque, that the rays of the sun cannot penetrate them.

There may be another reason: Pearl oysters are found in deep water and therefore need no protection from the rays of the sun, while *Ostrea cucullata* is frequently exposed and therefore possesses a very thick shell which does not allow the sun's rays to penetrate to the soft parts. Thus, while the inner structures are well protected, the marginal structures still need protection against light entering through the open edges of the shell-valves. Pigment is, therefore,

1. Hornell, James.—"The Anatomy of *Placuna placenta*," Marine Zoology of Okhamandal in Kathiawar, vol. I, 1909.

2. Herdman, W. A.—"The Anatomy of Pearl-oyster," Ceylon Pearl-oyster Fisheries and Marine Biology, vol. II, 1904.

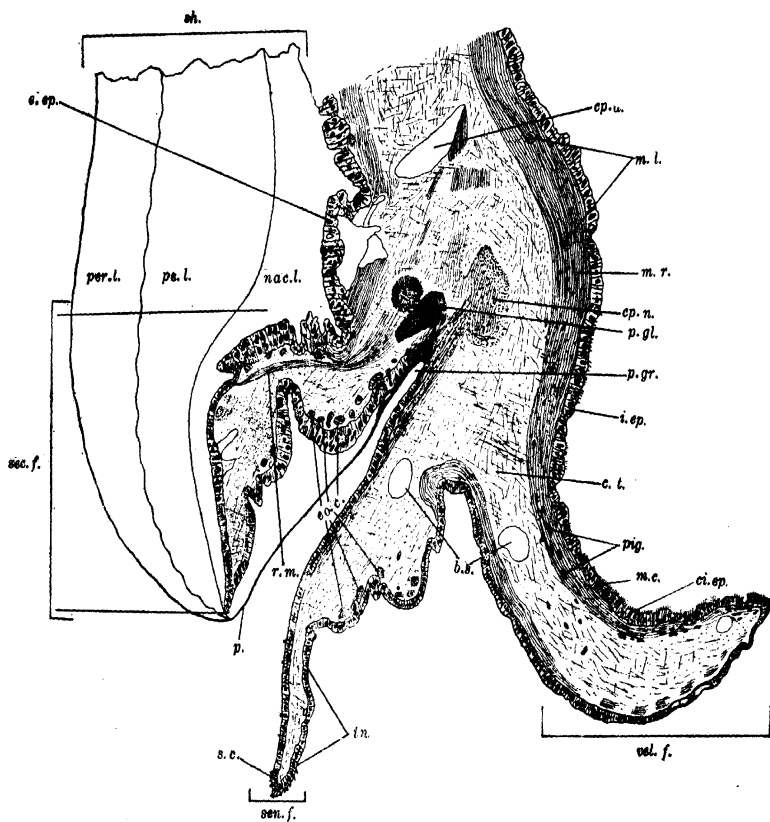


Fig. 7.—A transverse section across the shell and the edge of the mantle to show their relative positions. The shell (*sh.*) shows the three layers: the periostracal layer (*per. l.*), the prismatic layer (*ps. l.*), and the nacreous layer (*nac. l.*). The three folds of the mantle-edge are: the outer secretory fold (*sec. f.*), the middle sensory fold (*sen. f.*), and the inner velar fold (*vel. f.*). The cuticular periostracum (*p.*) lies in the periostracal groove and extends from the edge of the shell to the edge of the mantle between the secretory and sensory folds. *b. s.*, blood-sinuses; *c. t.*, connective tissue; *ci. ep.*, ciliated epithelium; *cp. a.*, circum-pallial artery; *cp. n.*, circum-pallial nerve; *e. ep.*, external epithelium; *eo. c.*, eosinophilous cells; *i. ep.*, internal epithelium; *m. c.*, mucus cell; *m. l.*, longitudinal muscle-fibres; *m. r.*, radial muscle-fibres; *pig.*, pigment; *p. gl.*, periostracal gland; *p. gr.*, periostracal groove; *r. m.*, pallial muscles attaching the mantle-edge to the shell; *s. c.*, sensory cells; *tn.*, tentacle. ($\times$ cir. 80).

developed on the edge and the inner surface of the mantle and also on the gills. In *Placuna placenta*, on the other hand, the shell is so thin and transparent as to allow the light to pass through, and therefore the pigment is developed on a larger scale than in the Bombay Oyster to protect the inner delicate structures from intense light.

The distribution of pigment on the mantle-edge is shown in fig. 7. Generally it forms dirty-yellow or brown patches but the margin often shows a black pigment which becomes lighter on the inner surface of the mantle, while occasionally a tinge of purple is also met with.

THE MUSCLES

The most important muscles of the body are the adductor, the pallial, the branchial and the cardiac.

The Adductor Muscle.

There is only a single posterior adductor muscle in *Ostrea* (figs. 4 and 5), the anterior adductor being altogether absent. The oyster is therefore a monomyarian like the pearl-oyster and other Eulamellibranchia. This muscle is situated subcentrally nearer the posterior than the anterior margin and stretches in an obliquely transverse direction, from one valve of the shell to the other. The pericardium, the heart and the visceral mass lie anterior to it, while the last portion of the rectum runs along its dorsal side. The parieto-splanchnic ganglia are situated on its ventral curvature. In section, its outline is oval or bean-shaped, with the concavity facing anteriorly and its broader convex face turned towards the posterior end. The impression of the muscle on the left valve is slightly larger than that on the right owing to the fact that the muscle-fibres are compactly grouped together on the right valve while they are stretched out obliquely on the left. This asymmetrical development of the adductor muscle may possibly be a cause of the asymmetry of other structures lying near it.

This muscle is not a homogeneous mass but consists of two distinct areas (figs. 4 and 5) which can be easily distinguished with the naked eye. The larger posterior area is made up of loose, opaque-white fibres, while the smaller anterior area consists of densely packed fibres which are flesh-coloured and translucent in appearance.

Under the microscope, the smaller portion is seen to be made up of bundles of smooth fibres enclosing empty spaces or lacunae. These fibres run straight through without any branching, from one valve to the other. The bundles of fibres contained in the bigger posterior portion, on the other hand, lie close together, there being no empty spaces or lacunae but just a few blood vessels scattered amongst them. The fibres show distinct branching and anastomosis and always have a greater affinity for stains than those of the smaller portion. The nuclei are seen distinctly along the margins of each bundle of fibres in both portions of the adductor muscle.

All the blood in the posterior aorta goes exclusively to the adductor muscle which has consequently an abundant blood supply. Within the muscle, there are a large number of lacunar

spaces filled with blood, which, together form the so-called *muscle-sinus*. A pair of adductor nerves arising from the parieto-splanchnic ganglia innervate the muscle.

The pallial muscles.

The pallial muscles consist of radial as well as longitudinal muscles. They are best developed at the margin of the mantle (fig. 7) and lie within the loose connective tissue separating the outer and inner epithelial lining of the mantle-lobe. The radial muscle-fibres are arranged in bundles and run at right angles to the long axis of the mantle-lobes, some of the bundles being inserted on the inner surface of the shell-valve along the pallial line (fig. 7). The longitudinal muscles are also developed best in the margin of the mantle. They consist of non-striped fibres which run parallel to the edges of the mantle-lobes along their whole length.

The branchial muscles.

The attached base of each ctenidium contains a cord of branchial muscles (fig. 9) running longitudinally along its axis. This axial cord gives off muscle-fibres to the lamellae and the filaments of the gills.

The cardiac muscles.

The cardiac or heart-muscles (fig. 30) are better developed in the ventricle than in the auricles. The muscle-fibres cross and re-cross each other in all directions, so that the wall of the ventricle has a spongy texture. All the heart-muscles are non-striped.

The muscles of the alimentary canal and those of the visceral mass and other organs will be described later.

THE GILLS OR BRANCHIAE

The oyster has a pair of highly developed *branchiae* or *gills*, each consisting of two gill-plates formed from the descending and ascending limbs of the filaments (fig. 8). It is this peculiar modification of the ctenidia into plates which has suggested the name *Lamellibranchiata* for the class to which the oyster belongs.

The gills are easily exposed by cutting off the mantle-lobes after the removal of the shell. They consist of four parallel folds which extend in a slight curve from the labial palps to the extreme posterior end of the mantle. While their distal edges hang freely in the mantle-cavity, the bases of the gills are fused anteriorly with the ventral margin of the visceral mass and extend backwards below the adductor muscle right up to the posterior mantle-suture. The posterior portions of the gills are attached to the sides and edges of the two mantle-lobes, thus forming a kind of horizontal partition between the large *infra-branchial* or *inhalent chamber* below, and the small *supra-branchial* or *exhalent (cloacal) chamber* above (fig. 5).

The single gill or *ctenidium* of each side is composed of two folds or plates called the *gill-plates* or *demi-branchs* arising from a common gill-axis (figs. 8 and 9). There is thus an outer and an inner gill-plate on each side of the body. Further, each gill-plate is V-shaped in section and is made up of two *lamellæ* corresponding to the two limbs of the V, one of them descending from the gill-axis and the other ascending. Each gill-plate encloses a space between its two lamellæ called the *inter-lamellar cavity*. Fig. 8 is a diagrammatic representation of the two gills showing the descending and ascending lamellæ of the two gill-plates of each ctenidium, the four lamellæ of each gill together presenting the figure of a W in section.

. The common gill-axis (figs. 8 and 9) of a ctenidium, from which the two gill-plates arise, is a dorso-ventrally stretched ridge made up of loose connective tissue traversed by a few muscle fibres. The outer epithelium consists of a single layer of cubical cells enclosing the connective tissue through which run the branchial nerve and the efferent vessel, one lying immediately above the other. The branchial nerve gives off small nerve-fibrils to the gill-filaments, while the efferent vessel shows apertures at intervals leading into the inter-lamellar septa.

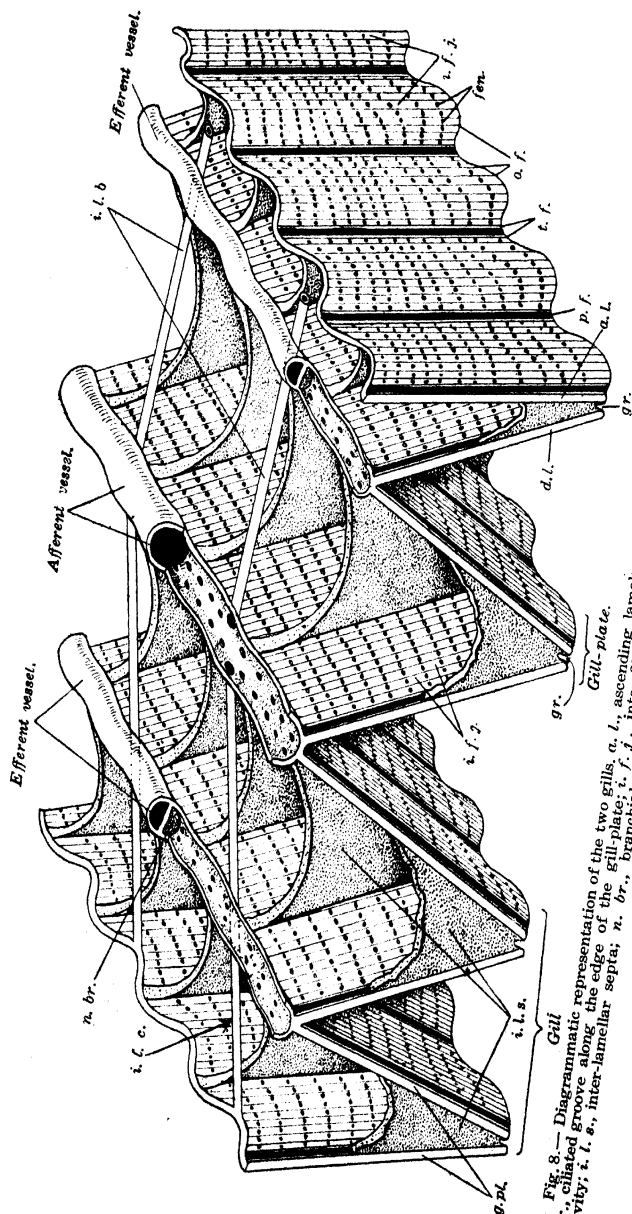


Fig. 8.—Diagrammatic representation of the two gills, *a. l.*, ascending lamella; *d. l.*, descending lamella; *fen.*, fenestrae; *g. pl.*, gill plate; *g. r.*, gill rakers; *i. l. s.*, inter-lamellar septa; *n. br.*, branchial nerve; *i. l. c.*, inter-lamellar cavity; *i. l. b.*, inter-lamellar bars; *i. l. j.*, inter-filamentous junctions; *i. f.*, ordinary filament; *p. f.*, principal filament; *t. f.*, transitional filament.

Each gill-plate is formed by the union of a long row of vertical V-shaped bars or *filaments* which are delicate tubular structures, arranged at right angles to the long axis of the ctenidium. Each filament starts from the gill-axis as its prolongation and is reflected on itself at the free edge of the gill-plate in such a manner that the ascending portion of the filament diverges

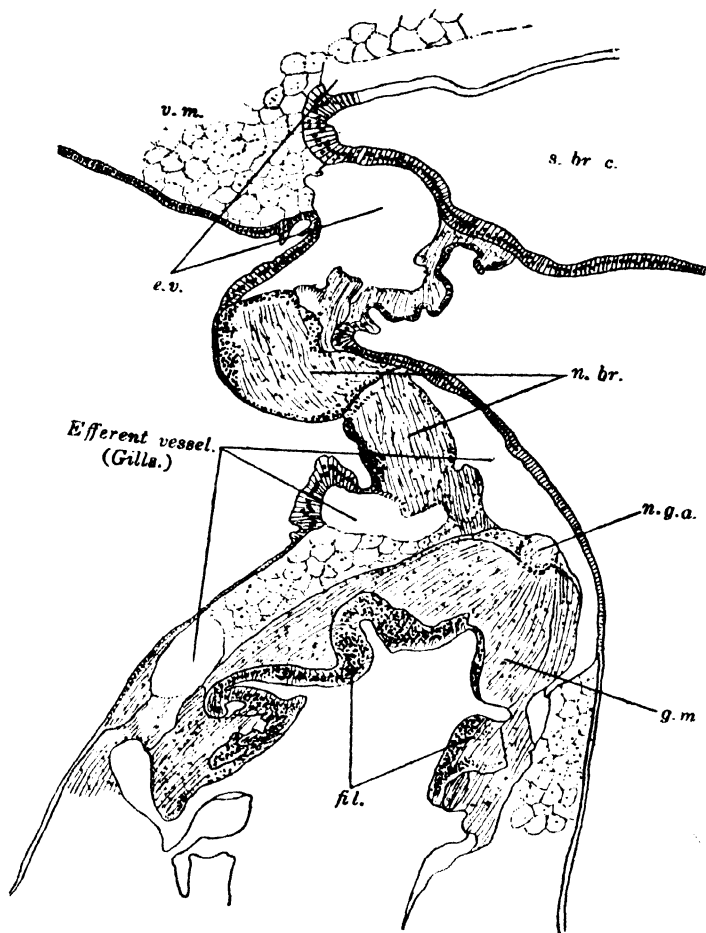


Fig. 9.— A transverse section passing through the gill-axis, showing the entrance of the branchial nerve and the exit of the efferent vessel. *e. v.*, efferent vessel in the visceral mass; *fil.*, gill-filament; *g. m.*, muscles of the gill; *n. br.*, branchial nerve; *n. g. a.*, nerve of the gill-axis; *s. br. c.*, supra-branchial cavity; *v. m.*, visceral mass. ($\times$ cir. 80)

from the descending while reaching the level of the gill-axis (fig. 8). These filaments, however, do not all lie in the same plane but are so arranged at different levels that each resulting lamella is thrown into a series of transverse folds or *plicæ*. The surface of each gill-lamella thus presents a pleated appearance and shows alternate grooves and ridges (fig. 11). Gills possessing *plicæ* or folds form a distinct type called the *plicate type*. The filaments themselves forming the lamellæ vary

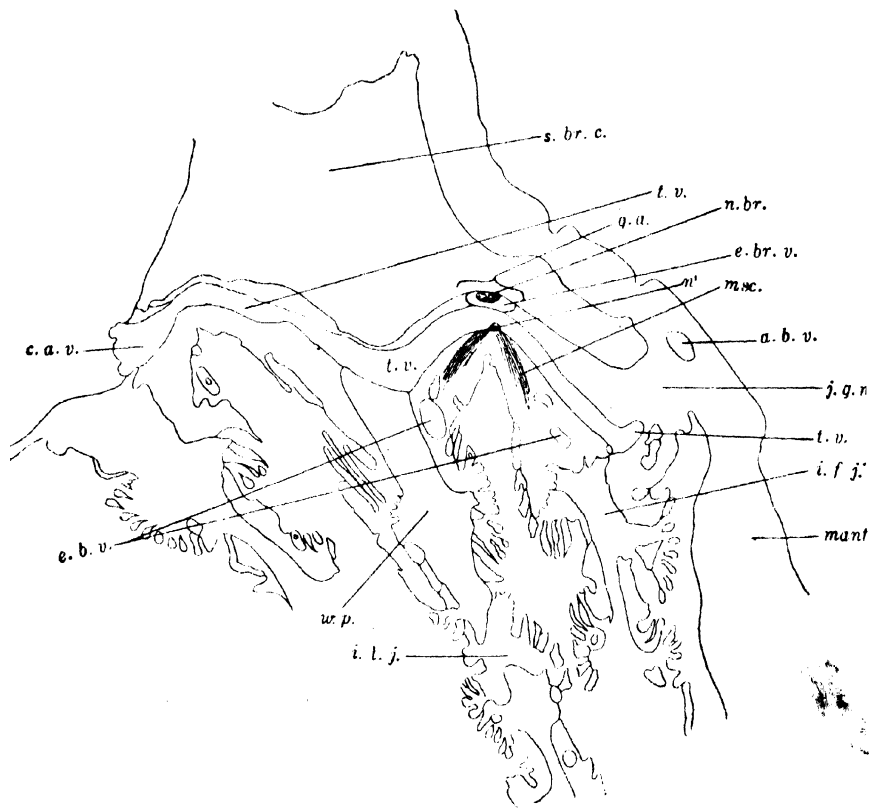


Fig. 10.—A transverse section through the gill-axis showing the junction of the gill with the mantle. *a. b. v.*, afferent blood-vessel; *c. a. v.*, common afferent vessel; *e. b. v.*, branches of the afferent blood-vessel; *e. br. v.*, branchial efferent vein; *g. a.*, gill-axis; *i. f. j.*, inter-filamentar junction; *i. l. j.*, inter-lamellar junction; *j. g. m.*, junction of the gill with the mantle; *mant.*, mantle; *m. sc.*, gill-muscles; *n. br.*, branchial nerve; *n'*, branch of the branchial nerve; *s. br. c.*, supra-branchial cavity; *t. v.*, transverse vessel; *w. p.*, water-pore. ($\times$ cir. 78.)

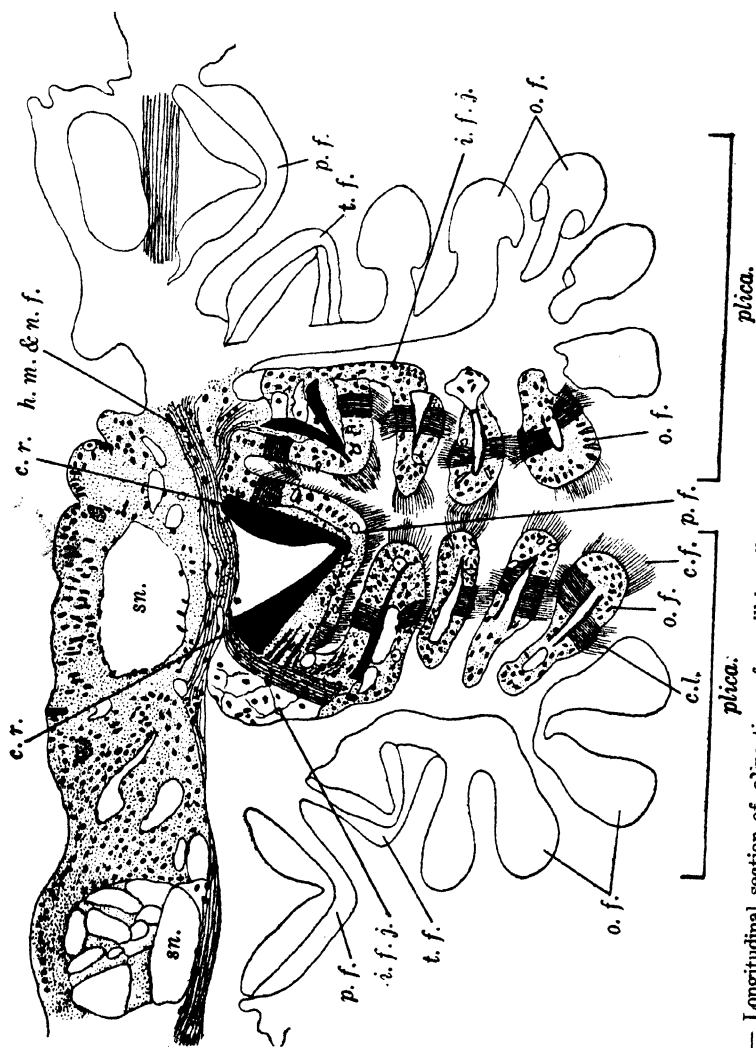


Fig. 11.— Longitudinal section of a portion of a gill-lamella showing two plicæ enclosing a groove and the three types of filaments. *c. l.*, lateral cilia; *c. f.*, frontal cilia; *c. r.*, chitinous rod; *h. m. & n. f.*, horizontal muscle-fibres and nerve fibres; *i. f. j.*, inter-filamentar junctions; *o. f.*, ordinary filament; *p. f.*, principal filament; *sn.*, blood-sinus; *t. f.*, transitional filament. ($\times$ cir. 155).

in size and structure. Those lying in the grooves between adjacent folds or plicæ are larger and are known as *principal filaments*, while the filaments forming the folds or plicæ themselves are small and are known as *ordinary filaments*. A third type of filaments called the *transitional filaments* lie in pairs, one on each side of a principal filament. These are intermediate in size between the principal and ordinary filaments. Gills consisting of several types of filaments are known as "*hetero-rhabdic*" as distinguished from "*homo-rhabdic*" gills in

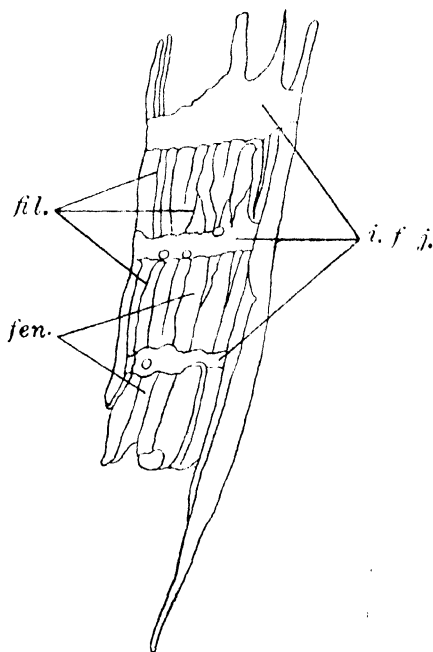


Fig. 12. — Horizontal section of a plica showing inter-filamentar junctions and fenestrae. *fen.*, fenestrae; *fil.*, filaments; *i. f. j.*, inter-filamentar junctions. ($\times$ cir. 64)

which, as in *Mytilus*, all the filaments are of one kind. This distinction between the three kinds of filaments is, however, secondary, since in the young oysters no principal or transitional filaments are developed.

• Fig. 11 represents a portion of a longitudinal section of a gill-lamella showing two folds or plicæ with a groove between them. At the bottom of the groove lies the principal

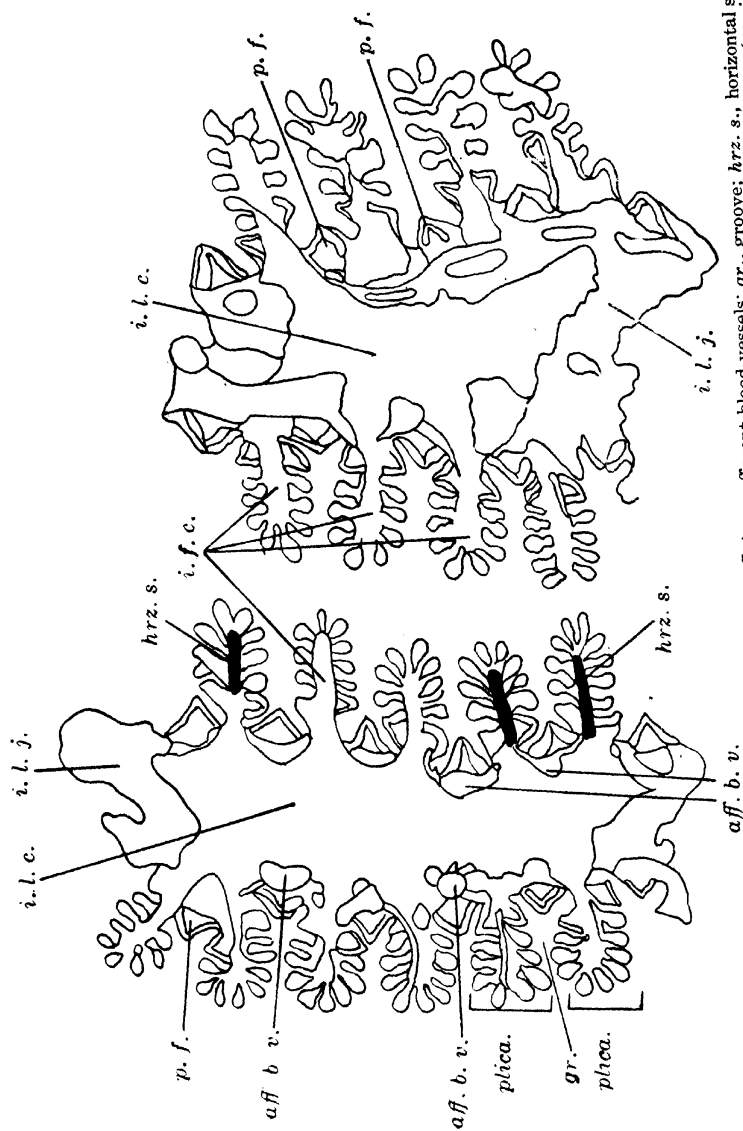


Fig. 13.—Transverse section of the filaments at two different levels. *aff. b. v.*, afferent blood-vessels; *gr.*, groove; *hrz. s.*, horizontal septum; *i. f. c.*, intra-filamentary cavity; *i. l. c.*, inter-lamellar septum or junction; *p. f.*, principal filament. ($\times$ cir. 120).

filament, while 9 to 12 ordinary filaments are united with one another at their bases through *inter-filamentar junctions* (fig. 12) to form a complete fold or plica. The inter-filamentar junctions are formed of loose vascular connective tissue and occur at short intervals regularly throughout the whole length of the filaments. They enclose openings called "*fenestræ*" through which water taken in by the animal flows towards the supra-branchial chamber. Each *lamella* thus consists of a series of filaments lying side by side and joined together by inter-filamentar junctions, but perforated by numerous fenestræ (fig. 12). As each gill-plate consists of two lamellæ, an outer and an inner, these lamellæ are also bound to each other by a series of *inter-lamellar junctions* (fig. 13), which run across from one lamella to the other in the form of septa, through which blood-vessels traverse the gills. These inter-lamellar junctions or septa occur only in relation to the principal filaments but the order is not regular throughout.

Towards the free edges of the gills, inter-lamellar septa are developed in connection with every principal filament of a plica but higher up towards the bases or axes of the gills, the septa are seen to occur in relation to every alternate principal filament; about the middle of the gill area, every fourth principal filament has an inter-lamellar septum while near the gill-axis, a septum is present only in connection with every sixth filament.

• Besides these septa, there are hollow *inter-lamellar bars* (figs. 8 and 10) formed of loose connective tissue, that run at short intervals across the floor of the supra-branchial chamber from one lamella to the other as well as from the outer lamellæ to their respective mantle-lobes (fig. 10). The inter-lamellar cavity is thus divided into water-pores or channels opening above into the supra-branchial chamber.

In a transverse section, an ordinary filament (fig. 14) appears as a club-shaped structure broad externally and narrow internally. Cells at the external or frontal end are large and cubical in shape and are provided with short *frontal cilia* while the cells lining the narrow inner end are small and non-ciliated. At the two corners of the broad end of each filament occur cells bearing *fronto-lateral cilia*, while two prominent cells lying along the sides of each filament bear long *lateral cilia*. It is these cilia which set up in-going currents of water on the gills. A number of mucus-gland-cells are also generally found on the free external border of a filament. These cells secrete mucus which entangles particles floating in the

water and prevents them from passing through the gills. Internally, the filament is hollow and its cavity is filled with phagocytes and connective tissue cells. The wall of the filament is supported by two delicate chitinous rods which meet at the frontal end but diverge at the other. The filamentary cavity is not divided by any transverse septum as in *Pecten*.

A principal filament (fig. 11) differs from an ordinary filament in size and shape. In sections, it is large and broad and

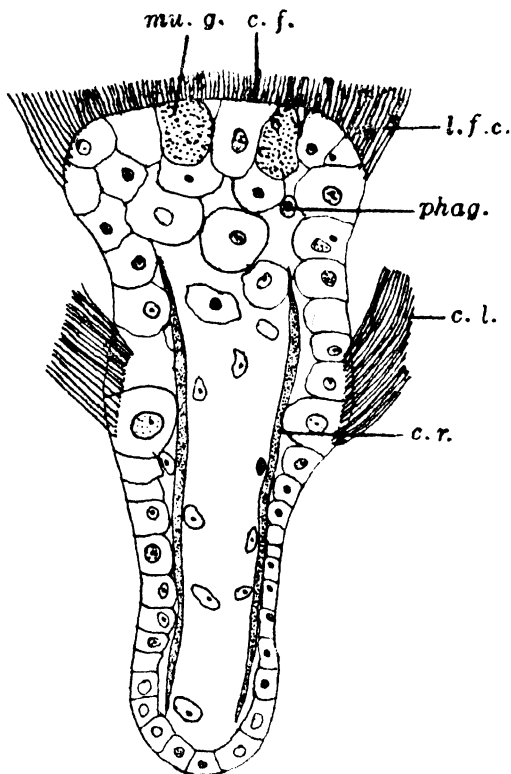


Fig. 14.— A section across a typical gill-filament. *c. f.*, frontal cilia; *c. l.*, lateral cilia; *c. r.*, chitinous rod; *l. f. c.*, latero-frontal cilia; *mu. g.*, mucus gland; *phag.*, phagocyte. ($\times$ cir. 900.)

has the shape of a triangle with its base placed against the inter-lamellar septum and its apex lying free in the groove between two adjacent plicae. The supporting chitinous rods are fused with each other at the apex but are widely separated at the base enclosing a small cavity. A narrow vascular tube

runs all along the base of the filament. The cilia are long and lie along the internal apical end of each filament.

The lower free margin of each gill-plate bears a more or less V-shaped groove all along its length (figs. 14 and 15). The groove is lined by ciliated epithelium and the cilia produce currents which carry foreign particles engulfed in the mucus towards the labial palps.

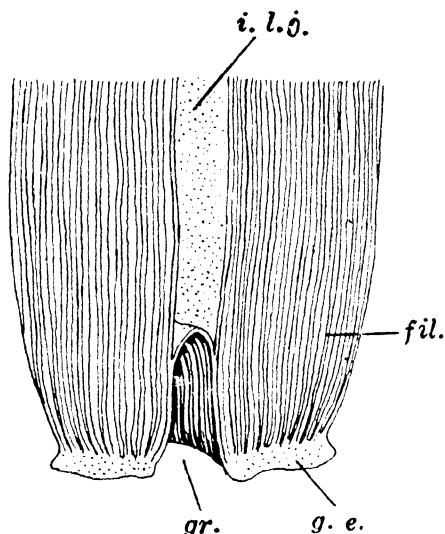


Fig. 15.— Diagrammatic representation of a part of the free edge of a gill. *fil.*, filament; *g. e.*, edge of the gill; *gr.*, ciliated groove; *i. l. j.*, connective tissue of the inter-lamellar junction.

The interlocking ciliated discs found in the filaments of *Anomia* and *Placuna placenta* are absent in *Ostrea*, in which the filaments are organically connected with one another by *inter-filamentar junctions* (fig. 9) only. These junctions have well-developed horizontal muscle-strands as well as a few vertical muscle fibres and some blood-lacunae. Gills with organic inter-filamentar junctions are known as "*synpto-rhabdic*" as opposed to "*eleuthero-rhabdic*" gills, which have only interlocking ciliated discs.

The gills of *O. cucullata* are remarkable in that they exhibit an extreme degree of concrescence of the lamellae amongst themselves as well as with the visceral mass and the mantle. At the anterior end, the apices of the gills are attached to the bases of the labial palps; the parts of the gills lying ventral to the labial palps are united with the visceral mass; but a little further back, the two innermost lamellae of the two gills are fused not only with each other but

also along their common axis with the visceral mass. This fusion extends for a short distance and is soon supplemented by the union of the outer gill-plates with the mantle (fig. 10). This extends as far as the place of entrance of the branchial nerve into the gill, behind which the axis of the ctenidium becomes detached from the body. The gills are held in position by the fusion of the extremities of the outer lamellae of the outer gill-plates with the mantle-lobes. The posterior apices of the gills are joined with each other and with the mantle-lobes. As a result of this conrescence of the gills,

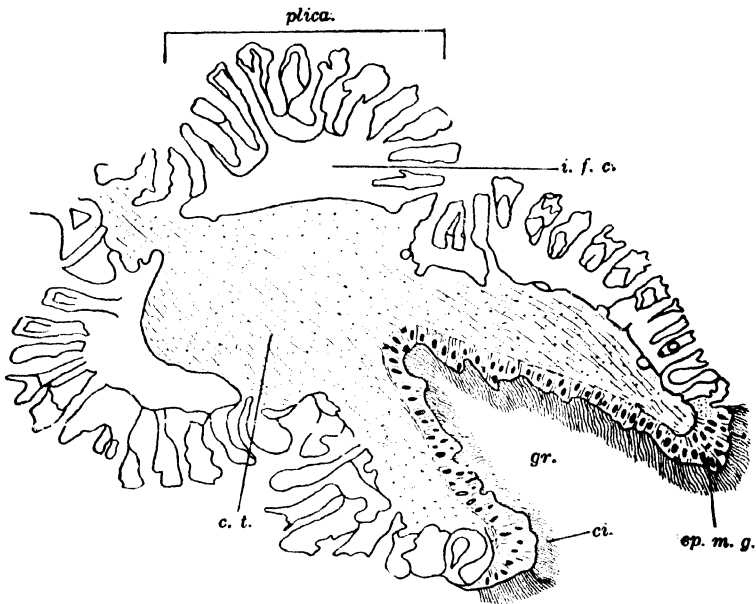


Fig. 16.— A section across the free edge of a gill. *c. i.*, cilia; *c. t.*, loose connective tissue with nerve and muscle fibres; *ep. m. g.*, marginal epithelium of the gill; *gr.*, ciliated groove; *i. f. c.*, intra-filamentary cavity. ($\times$ cir. 80).

the water-current can pass from the inhalent to the exhalent chamber only through the fenestrae amongst the filaments.

The branchial nerve arising from the parieto-splanchnic ganglia runs throughout the axis of each gill (figs. 9 and 10) and gives branches to the filaments at short intervals. In sections, these nerve-branches can be seen in the filaments lying between the outer epithelium and the chitinous rods. Both the gill-axis and the filaments have well-developed muscles.

The gills of the oyster are not only respiratory in function but are also important food-catching organs. The lateral cilia of the filaments cause a strong in-going current of water into the branchial chamber whence it is forced through the fenestrae lying between the gill-filaments into the *intra-filamentar cavities* (figs. 13 and 16) and thence into the inter-lamellar water-pores. The water then passes into the supra-branchial chamber by the force of the in-coming current and is carried to the exterior through the exhalent chamber. A current of fresh oxygenated water is thus kept up continually through the gills. In this way the blood brought to them by the common and lateral afferent veins is aerated and any infusoria, diatoms and other minute organisms contained in the water are caught by the cilia in the grooves at the edges of the gills. They are then entangled in the mucus and passed forwards to the labial palps and the mouth.

It is important to note that the anterior end of each gill is enclosed within the ventral edges of the labial palps thus forming a kind of gutter (fig. 17) between the palps along which food-particles are carried to the mouth. The gills of *O. cucullata*, unlike those of other Lamellibranchs, do not serve as brood-pouches for the eggs of the female, since fertilisation and development take place outside the body in the open sea.

THE ALIMENTARY CANAL

The organs concerned with the collection, digestion and absorption of food comprise the gills, the labial palps, the mouth, the œsophagus, the stomach, the intestine and the rectum, as well as the digestive diverticula, the crystalline style sac and the pyloric cæcum. The greater part of the alimentary canal lies within the visceral mass and is easily dissected out in specimens hardened in 5% formalin.

The "*gills*" or *ctenidia*, believed at one time to be purely respiratory in function, are now recognised to be primarily food-catching organs. The lateral cilia of the gills (fig. 14) produce an in-going current of water carrying microscopic organisms together with the detritus suspended in sea-water into the inhalent chamber¹. As the in-going current passes through the narrow inhalent aperture, its speed is reduced and thereby larger particles of food in suspension drop on to the mantle-folds and never reach the gills. But the smaller particles are carried further and are deposited on the surface of the gills which serve as very efficient filters, allowing the water to pass through the fenestræ between the filaments, but retaining the food particles on their surface. These are entangled in the mucus secreted by the mucus-glands covering the surface of the gill-filaments and are carried by the cilia of the principal filaments to the free margin of the gill. Here the small particles of food along with thin strings of mucus secreted in the ciliated groove are carried to the labial palps, while the larger particles of food or heavily laden mucus-strings fall out of the groove (figs. 15 and 16) on to the mantle surface and are finally expelled. This sorting out of the food particles is also brought about by muscular contraction and bending of the gill-filaments. In fact, the arrangement of the ciliary currents on the gills, along with their muscular contractions, forms a very efficient sorting mechanism whereby all small debris is strained off and passed on to the labial palps and the mouth (fig. 17), while the larger particles are side-tracked and ejected.

1. Although the two mantle-lobes are free all along the ventral margin, the food current is not drawn in along the whole length of the inhalent chamber, since the mantle-folds are normally apposed, except for a short distance on the ventro-posterior margin of the animal (fig. 5) (Yonge).

The *labial palps* (figs. 4 and 17) are large triangular flaps lying in front of the gills and attached to the visceral mass by a broad base. There is a pair on either side of the mouth called the *external* and *internal labial palps*. The external palps unite with one another in front of the mouth while the

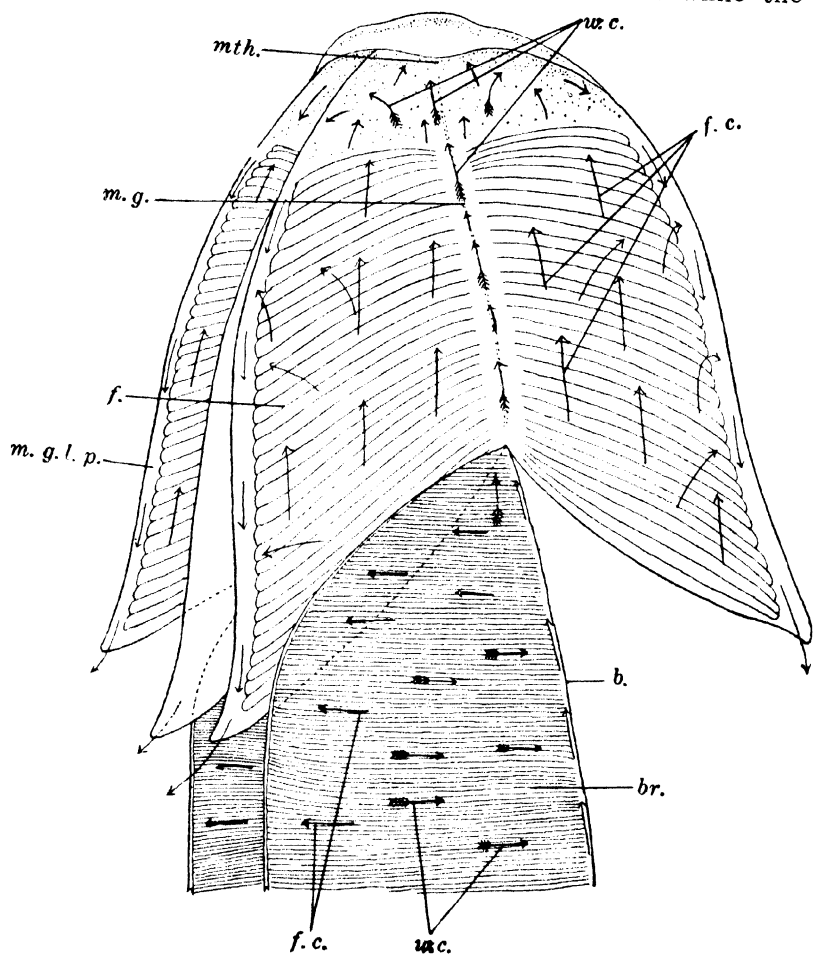


Fig. 17.—A diagram showing the junction of the labial palps and gills and the direction of food and water-currents on them. *b.*, base of the gill; *br.*, gill; *f.*, furrow on the labial palp; *f. c.*, direction of the food-current; *m. g.*, median gutter; *m. g. l. p.*, marginal groove of the labial palp; *mth.*, mouth; *w. c.*, direction of the water-current. (× cir. 9.)

internal palps are similarly united behind the mouth. The outer surfaces of these palps are smooth but the inner opposing surfaces bear grooves and ridges (figs. 17 and 18). At the junction of the two palps on each side, there is a large *palpal gutter* (fig. 17) which receives numerous fine ciliated groovelets, running across the inner surfaces of the palps. The ridges or folds separating the groovelets gradually increase in height towards the free margin of the palps and are generally slightly inclined towards the mouth.

In sections, the labial palps (fig. 18) are seen to consist of a core of connective tissue covered on both sides by columnar epithelium which is

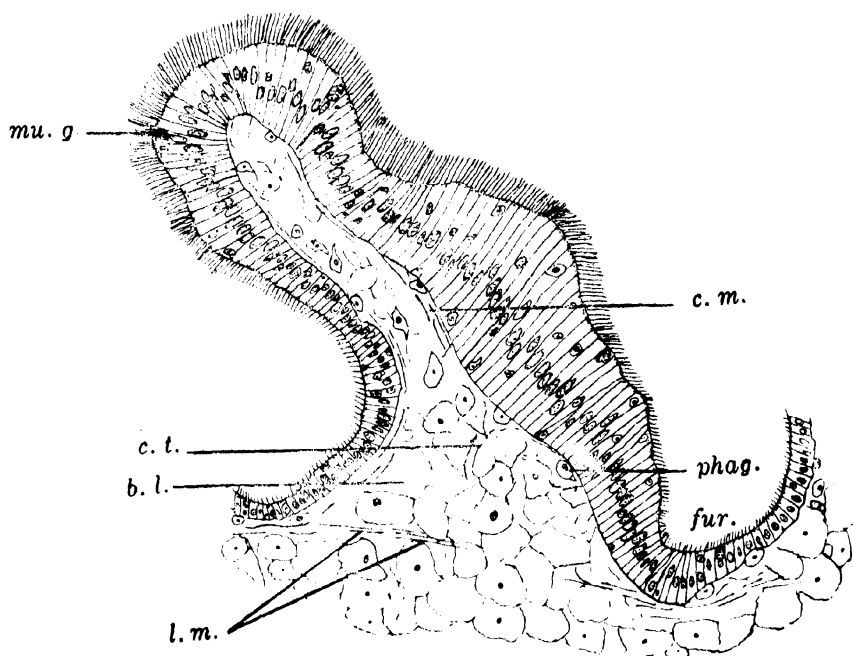


Fig. 18.—Transverse section through a fold on the inner face of a labial palp. *b. l.*, blood-lacuna; *c. m.*, circular muscles; *c. t.*, connective tissue; *fur.*, furrow between two adjoining folds; *l. m.*, longitudinal muscles; *mu. g.*, mucus gland cell; *phag.*, phagocyte. ($\times$ cir. 900)

underlined by a basement membrane. The epithelium covering the inner surface consists of tall narrow cells provided with cilia, the cells becoming shorter towards the base of the palp. Numerous large phagocytes are present amongst the epithelial cells, while a few unicellular mucus glands are seen in the

underlying connective tissue of the crest of ridges. The epithelium of the smooth outer surface, on the other hand, consists of small narrow cells of which only some possess minute cilia while the others are non-ciliated. The ciliated cells appear to be sensory in function. Unicellular mucus glands are as numerous in the epithelium of the outer surface as in that of the inner. The connective tissue supporting the palps consists of large vesicular cells interspersed with blood-spaces and surrounded by circular and longitudinal muscle-fibres which lie immediately beneath the basement membrane.

The food substances reaching the inner surface of the palps from the free margins of the gills are again most rigorously sorted out here, so that only the smallest particles cross over to the mouth, while all the other particles are rejected.

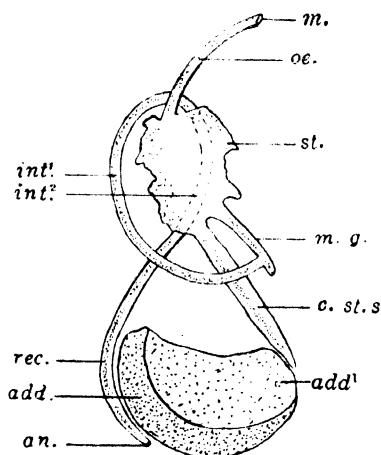


Fig. 19.—The alimentary canal of the larval oyster. *add.*, the posterior part of the adductor muscle; *add*¹., the anterior part of the adductor; *an.*, anus; *c. st. s.*, crystalline style sac; *int*¹., the ascending limb of the intestine; *int*²., the descending limb of the intestine; *m.*, mouth; *m. g.*, mid-gut; *œ.*, oesophagus; *rec.*, rectum; *st.*, stomach. ($\times$ cir. 20)

In order to follow easily the course of the alimentary canal and the disposition of its component parts in the adult, it will be better to describe first the simple digestive canal of the larva. Reference to fig. 19 shows the *mouth* leading into a long *oesophagus* which enlarges to form the *stomach*. The stomach shows several small irregular processes projecting out from its walls besides an elongated blind cæcal outgrowth, the rudiment of the *crystalline style sac*, which arises from the posterior end

of the stomach. Close by, the *mid-gut* also takes its origin from the stomach and leads into the *intestine* which makes a loop round the stomach and forms an *ascending* and a *descending limb* of the intestine. The intestine continues backwards into the *rectum*, which opens into the supra-branchial chamber through the *anus*. We may note here that the gut of the veliger larva is lined with ciliated epithelium throughout its whole length.

In the adult, the *mouth* is a transverse slit-like opening at the anterior end of the body bounded by two pairs of labial palps. The epithelium of the mouth is quite distinct from that of the labial palps and consists of tall columnar cells provided with *short cilia* with no mucus-glands¹ amongst them. The mouth leads into a long *oesophagus*, the lumen of which is compressed dorso-ventrally and appears as a narrow slit in transverse sections. The inner epithelial lining consists of tall and narrow ciliated cells with no mucus glands, while the surrounding connective tissue contains numerous muscle-strands as well as blood-spaces. The lumen of the oesophagus becomes narrow as it passes backwards and upwards to enter the dorsal region of the stomach.

The *stomach* is a large sac occupying a central position in the visceral mass. It is difficult to follow the outline of the stomach by a dissection, as it is surrounded on all sides by the tubules of the digestive diverticula and its internal wall is thrown into a complicated system of grooves and ridges. Yonge² obtained casts of the stomach by injecting into it a warm concentrated solution of gelatine through the oesophagus. We have made similar casts by injecting hot paraffin or a mixture of paraffin and resin coloured with particles of carmine. These casts are dissected out after they become solid.

Fig. 20 shows a paraffin cast of the stomach and its outgrowths viewed from the left side of the animal. The outgrowths of the stomach include the *dorsal and ventral pouches* situated on the left side of the stomach, a long posterior outgrowth called the *crystalline style sac* and a long

1. In *Ostrea edulis*, Yonge describes mucus glands in the epithelium of the mouth and also records the presence of *long cilia* on the epithelial cells.

2. Yonge, C. M.—“Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis*.”, Journ. Mar. Biol. Assoc., 14, 1926-27.

blind pouch, called the *pyloric caecum*, lying on the right side of the stomach. The *dorsal and ventral pouches*, of which the ventral is larger than the dorsal, are conical outgrowths connected with the stomach for a considerable distance and communicating with each other through a wide passage. These pouches are believed to be places for the storage of food. The

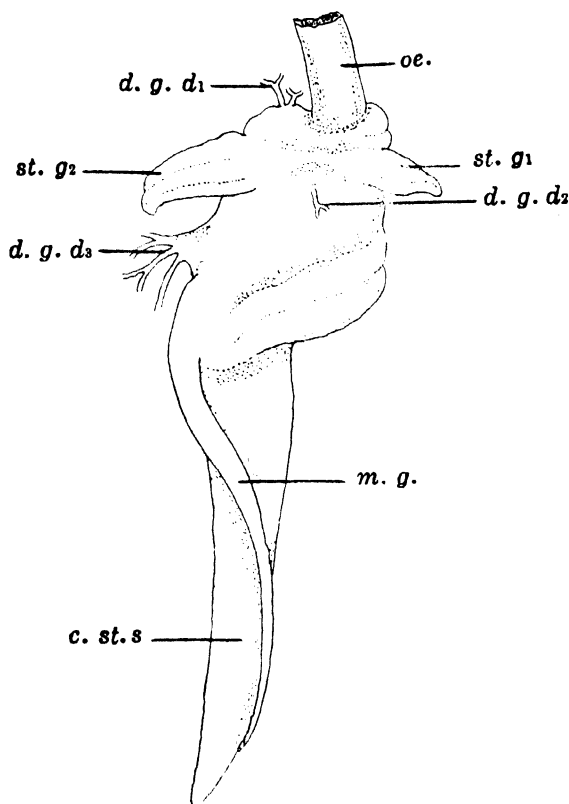


Fig. 20.—A cast of the stomach as seen from the left side. *c. st. s.*, crystalline style sac; *d. g. d¹*., *d. g. d²*., *d. g. d³*., first, second and third groups of ducts of the digestive gland; *m. g.*, mid-gut; *oe.*, oesophagus; *st. g¹*., *st. g²*., dorsal and ventral pouches of the stomach. ($\times$ cir. 16)

crystalline style sac is a large finger-shaped outgrowth of the stomach, wedged posteriorly into the visceral mass with its distal end placed near the antero-ventral border of the adductor muscle. Except for a short diverticulum at its origin

from the stomach, the style-sac is united along its entire length with the next section of the alimentary canal—the mid-gut.

The cæcum¹ originates from the right side of the stomach above its middle portion, and forms a very conspicuous outgrowth. As it passes forward, it divides into two separate pouches which lie at different levels and extend for a considerable distance on the right side of the body going anteriorly even beyond the mouth. They are always full of food-material and contain a large number of mucus cells in their inner epithelial lining.

The *digestive diverticula* form a brownish mass of blind tubules surrounding the stomach. They were termed "liver"

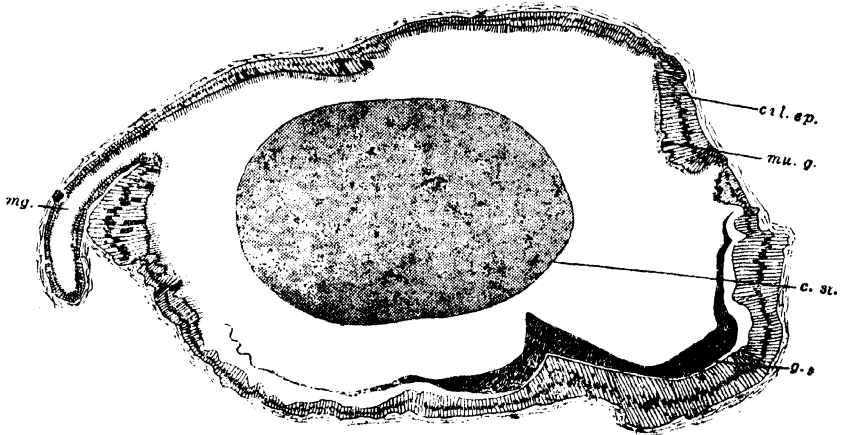


Fig. 21.—Transverse section of the posterior part of the stomach passing through the crystalline style sac and the mid-gut. The head of the crystalline style is cut and the gastric shield is seen lying against the left wall of the stomach. *cil. ep.*, ciliated epithelium; *c. st.*, crystalline style; *g. s.*, gastric shield; *mu. g.*, mucus gland-cells; *m. g.*, mid-gut. ($\times$ cir. 52)

or "hepato-pancreas" by various authors, but Yonge has recently shown that they have none of the functions of a true liver or pancreas but are really organs of assimilation and intra-cellular digestion. He has, therefore, suitably named them "digestive diverticula." Three groups of ducts (fig. 20) from the digestive

1. This structure has not been described by Yonge in *O. edulis*.

diverticula open into the stomach. The first group enters the anterior end of the stomach near the point of entrance of the œsophagus; the second opens near the middle line immediately behind the origin of the dorsal and ventral pouches; and the third, consisting of a very large number of ducts, opens on the ventral side of the stomach.

On opening the stomach, a cuticular structure of irregular shape is seen applied to its left wall. This is the *gastric shield* (fig. 21) which consists of two unequal portions joined together by a narrow isthmus (fig. 22). The smaller

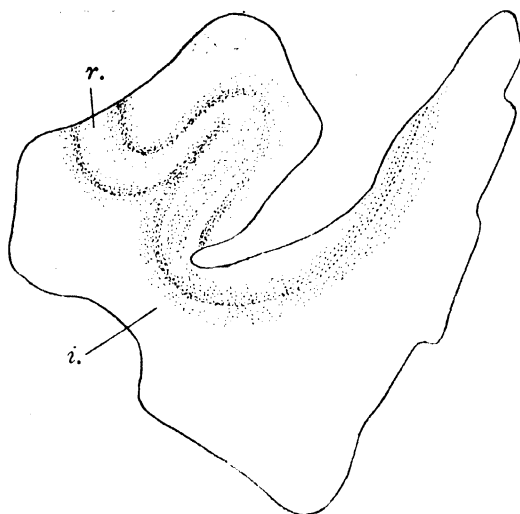


Fig. 22.—The gastric shield taken out of the stomach. *i.*, narrow isthmus joining the smaller thickened portion with the larger thin portion; *r.*, a ridge on the shield. ($\times$ cir. 45)

portion is much thickened and bears prominent ridges while the larger portion is thin and membranous. Fine striations and granular protuberances are seen in places but there are no teeth as have been found by Yonge in *O. edulis*. The grooves and ridges on the gastric shield really correspond to those on the inner wall of the stomach. It is difficult to interpret the complicated undulations on the wall of the stomach, but it has been suggested that they probably direct the food towards the

ventral side of the stomach whence the mid-gut takes its origin.

During life, the cavity of the *crystalline style sac* is completely filled by a gelatinous rod, the *crystalline style* (fig. 23). The style is a solid but flexible rod, about half an inch in length in a full-grown specimen. There is a distinct head and a tapering posterior end. The head of the style projects into the stomach and lies against the gastric shield (fig. 21). The colour of the style varies from pale yellow to light flesh, depending upon the nature of the food of the animal.

On removal of the animal from water, the style dissolves completely within a short time. The function of the style and its rapid dissolution have been subjects of discussion during recent years.

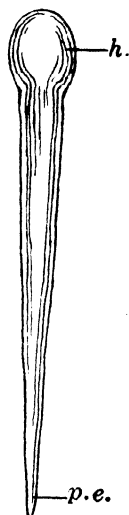


Fig. 23.— The crystalline style *h.*, head; *p. e.*, posterior pointed end. ($\times 6$)

Orton¹ has proved by a number of experiments that the style of *O. edulis* dissolves when the animal is removed from water but develops again when the animal is returned to sea-water. He holds that the dissolution and reformation of the style depend only on physical conditions, and that temporary starvation produces no effect on the presence or absence of the crystalline style. Yonge has confirmed Orton's results and states that the style is dissolved under abnormal conditions and is never absent in healthy individuals even when they are starved. He further states "that the disappearance of the style under abnormal conditions is probably due to the lowering of the vital activities, which include the secretion of the style by the less acid contents of the stomach." Berkeley² states that the style has a reserve of oxygen which is used in anaerobic respiration—a theory which is not fully substantiated in view of the fact that there is no correlation between the size of the style in different species and the nature of the habitat. Mitra, Dakin, Nelson and Boris have also worked on the crystalline style of various Lamellibranchs and have arrived at similar conclusions.

1. Orton, J. H.—Fishery Investigations. Series II, 6, No. 3, 1923.

2. Berkeley, C.—"On the Crystalline Style as a possible factor in the Anaerobic Respiration of certain marine Molluscs.", Journ. Exp. Zool., Vol. 37, 1923,

Histology of the Stomach and its Appendages.

The epithelial lining of the stomach (fig. 21) consists of cells which are more elongated and have longer cilia than those of the œsophagus. Mucus glands are abundant and the wandering phagocytes are numerous. But the epithelium lying next to the gastric shield is of a different type; it bears no cilia

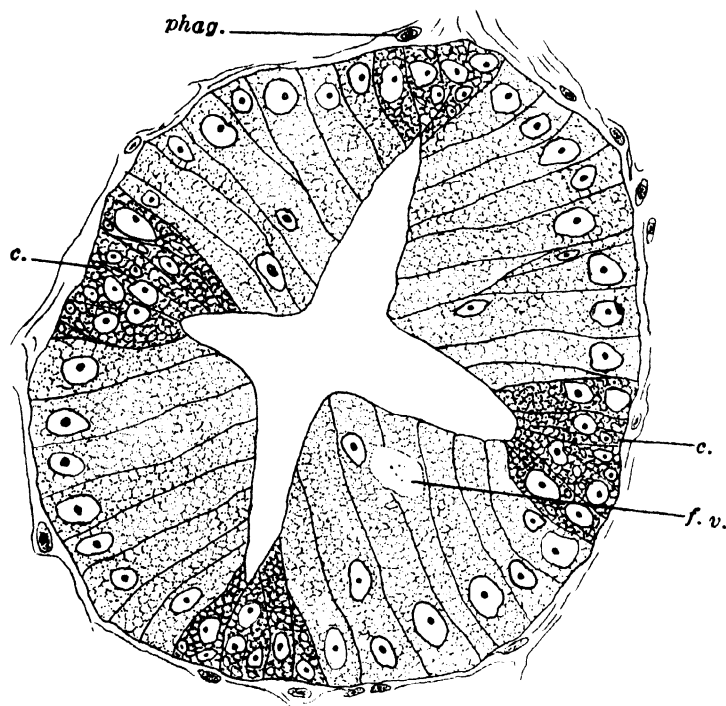


Fig. 24.— A transverse section through a digestive diverticulum. *c.*, a crypt containing darkly staining young cells; *f. v.*, food-vacuole; *phag.*, phagocyte. ($\times$ cir. 36)

and has no mucus glands. Yonge¹ emphasises the importance of phagocytes and says, "One of the most striking features about the gills, palps and the entire alimentary tract is the universal presence of wandering phagocytic cells. They are always easy to distinguish because their nuclei are small and

1. Yonge, C. M.—"Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis*", Journ. Mar. Biol. Assoc., 11, 1926-27,

spherical, containing a large number of fine granules of chromatin, which stain darkly with haematoxylin, unlike the nuclei of the epithelial cells which are oval and stain lightly. The presence of these phagocytes is characteristic of Lamellibranchs (with the possible exception of the Septibranchs) and attention has been drawn to their presence by many workers, although their great importance in the physiology of digestion in these animals has not always been recognized. There can be no doubt that the cells are amoeboid

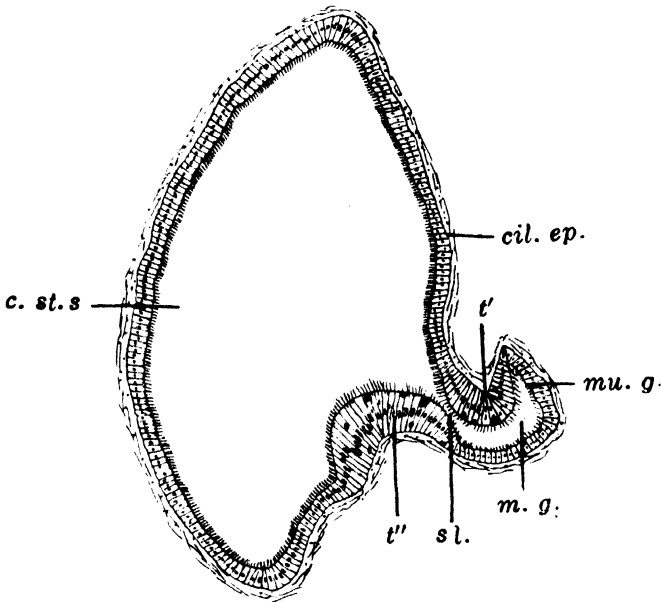


Fig. 25.— A transverse section through the junction of the crystalline style-sac and the mid-gut. *cil. ep.*, ciliated epithelium; *c. st. s.*, crystalline style-sac; *m. g.*, mid-gut; *mu. g.*, mucus gland; *sl.*, slit connecting the style-sac with the mid-gut; *t'*, larger typhlosole; *t''*, smaller typhlosole. ($\times$ cir. 40)

and wander freely through the tissues and in and out of the lumen of the gut and of the blood-vessels”.

The tubules of the digestive diverticula are usually circular in cross section while the lumen is in the form of a cross (fig. 24). The cells lining the cavity are irregular in shape and have an indistinct outline. They contain an oval nucleus with a conspicuous nucleolus lying towards the base of

the cell. There are no mucus glands or cilia on the cells, although food-vacuoles are present, sometimes with ingested food-material. Patches of darkly staining protoplasm with numerous nuclei are seen at the four corners of the cross—these are young developing cells. Phagocytes occur everywhere, while radial muscle-strands are sometimes found in the connective tissue surrounding the basement membrane. Yonge¹ has observed the presence of cilia in the fresh material of other Lamellibranchs and it is believed that all Lamellibranchs possess long cilia in the lumen of these tubules.

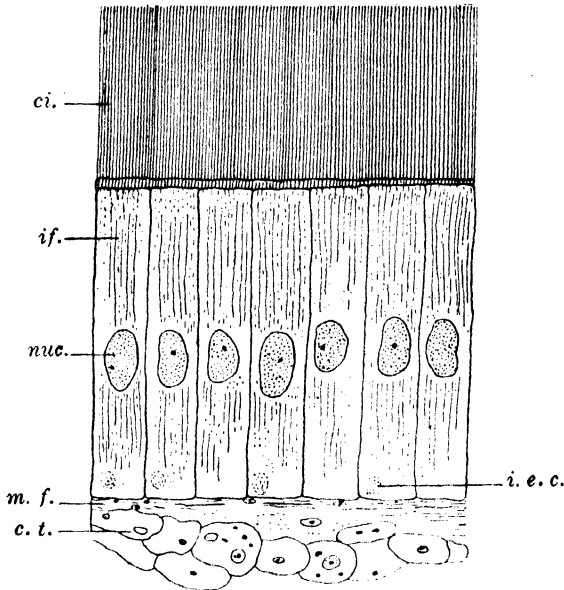


Fig. 26.— A part of the crystalline sac epithelium (highly magnified). *ci.*, cilia; *c. t.*, connective tissue cells; *i. e. c.*, intra-epithelial canal; *if.*, internal fibrillar apparatus; *m. f.*, muscle fibres; *nuc.*, nucleus. ($\times$ cir. 900)

The crystalline style sac is lined with large and regularly arranged columnar epithelial cells, having a large oval nucleus in the centre unlike those of *O. edulis* in which the nuclei are situated at the base. The cells are provided at their distal ends with long, stout, closely set cilia of almost equal length (fig 26). The cilia seem to be extremely stiff

1. Yonge, C. M.—“Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis*.” Journ. Mar. Biol. Assoc., 11, 1926-27,

and form a perfectly even surface upon which the style rests. No trace of mucus glands is seen in this epithelium.

Mackintosh² studied in detail the structure of the style and its sac in *Crepidula fornicata*, which, although a Gastropod, has a strikingly similar region as that of Lamellibranchs. Later Mackintosh and Yonge have shown that in *Ostrea edulis*, the cilia covering the epithelium are continued into the body of the epithelial cells where they form an "internal fibrillar apparatus." These fibres are greatly thickened below the nucleus and form a "bundle of thick rod-like bodies." Both these workers have also described a series of "intra-epithelial canals" at the bases of these cells, the function of which seems to be to give additional support to the epithelium, since it has to bear a considerable strain when the style is rotated and pushed forward.

The next portion of the alimentary canal, the *mid-gut*, originates from the stomach on the right side of the style-sac

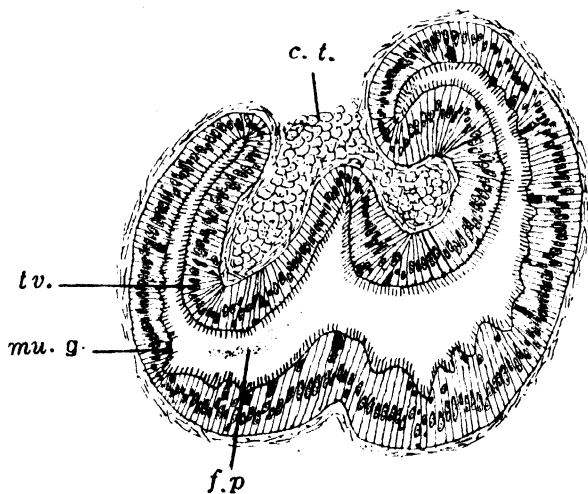


Fig. 27.—A transverse section of the mid-gut; *c. t.*, connective tissue; *f. p.*, food particles; *mu. g.*, mucus gland; *t. v.*, typhlosole. ($\times$ cir. 80)

(fig. 20), and turning round immediately to its left runs parallel to it all along its length; on reaching the distal end of the style-sac, the mid-gut or the *intestine*, as it is now called, turns anteriorly and runs completely back on its course. Passing along the dorsal surface of the stomach, it reaches the level of the œsophagus and then turns downwards

2. Mackintosh, N. A.—"The Crystalline Style in Gastropods.", *Quart. Journ. Micr. Sci.*, Vol. 69, 1925,

and backwards and encircles the stomach on the left side before passing into the rectum (fig. 19). The last part of the intestine, the *rectum*, runs independently on the dorsal side of the heart (fig. 5) and not *through* the heart as in other Lamellibranchs. The rectum ends in an oval opening, the *anus*, lying at the tip of a small papilla on the dorsal side of adductor muscle (fig. 4) and within the exhalent chamber.

The intestine is lined by an epithelium of ciliated cells throughout its length (fig. 27), and its absorptive surface is considerably increased by a double fold of the typhlosole. The latter, when seen in a transverse section, is very prominent

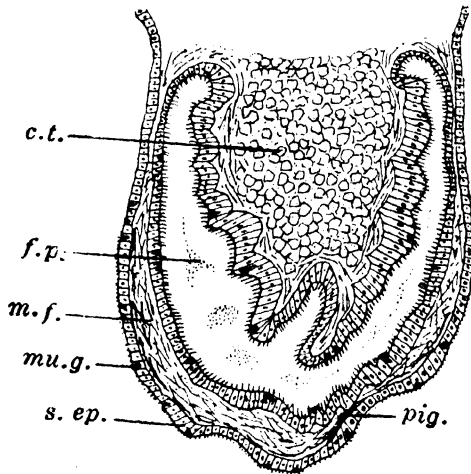


Fig. 28.— A transverse section through the rectum. *c. t.*, connective tissue of the typhlosole; *f. p.*, foecal particles; *m. f.*, muscle fibres; *m. g.*, mucus gland; *pig.*, pigment; *s. ep.*, surface epithelium. ($\times$ cir. 40)

with a deep groove in the centre and gives the intestine a characteristic appearance. Mucus glands are numerous but muscle fibres are absent around the epithelium.

In a cross section (fig. 28), the lumen of the rectum is very much reduced owing to the presence of the typhlosolar fold which is itself thrown into many smaller folds. Mucus glands are numerous, the basement membrane is well developed and the epithelium consists of ciliated cells. The outer surface

of the anal papilla is pigmented and contains ciliated cells, many of which are sensory.

The cavities of the style-sac and the mid-gut are united by a narrow slit all along the length of the style-sac. In sections, the two cavities communicate but are easily distinguishable, the small narrow chamber being that of the mid-gut and the larger circular cavity that of the style sac (fig. 25). The latter contains the crystalline style in living specimens (fig. 21).

It is interesting to note, however, that the style-sac and the mid-gut are quite separate in the larval stages and in the early stages of the adult. But there is always a marked groove on one side of the style-sac even in young oysters and it is probable that it is this groove that opens into the mid-gut in the adult.

THE BLOOD-VASCULAR SYSTEM

A study of the literature on *Ostrea* revealed the fact that our knowledge of the circulatory system of this form was incomplete; consequently, the blood-vascular system was studied in detail both by dissections and injections and further by an examination of serial sections.

The *blood* is a colourless fluid with a higher specific gravity than that of water and a strong saline taste. The blood corpuscles are small and colourless and are capable of amoeboid movements by means of their blunt pseudopodia. The corpuscles are .02 mm. in diameter and, in permanent preparations, show a prominent nucleus in the centre of a rounded or ovoid body.

The structures concerned with circulation are: (1) the heart enclosed in the *pericardium*, (2) the *arteries*, and (3) the *veins*.

The Pericardium.

The *pericardium* (fig. 5) is a thin-walled sac lying between the visceral mass in front and the adductor muscle behind. On its dorsal side, the pericardium is bounded by the proximal portion of the rectum and on its ventral side by the renal organs. The cavity of the pericardium is more spacious on the left side of the body than on the right, but the right portion is very much elongated and extends for a considerable distance along the anterior margin of the adductor muscle. The pericardial cavity encloses the heart and communicates with the renal organs through a pair of well-developed reno-pericardial canals (fig. 40). It is lined internally by a glandular epithelium containing a dark brown pigment which is also found in the walls of the auricles.

The Heart.

In most Lamellibranchia, the rectum perforates the heart and passes through it, but in *Ostrea*, the heart and the rectum remain apart, the heart lying beneath the rectum (fig. 4). The rate of heart beat is slow with an average of about 15 to 18 contractions per minute at the room temperature (80° F).

The *heart* (fig. 29) consists of a ventricle and two auricles, the ventricle being twice the size of the auricles. The *ventricle* is a large pear-shaped structure with spongy

muscular walls. It lies suspended obliquely by the roots of the aorta in the dorso-anterior region of the pericardium (fig. 5), and is slightly constricted along its middle line forming two well-marked unequal divisions, the left being slightly larger than the right. The muscular walls of the ventricle consist of non-stripped muscle-fibres, an underlying delicate basement membrane and an epithelial layer of cells (fig. 30, A and B). The ventricular cavity is traversed by bundles of muscle-fibres in such a manner that it may be said to be incompletely divided into two chambers, corresponding to its external divisions, thereby

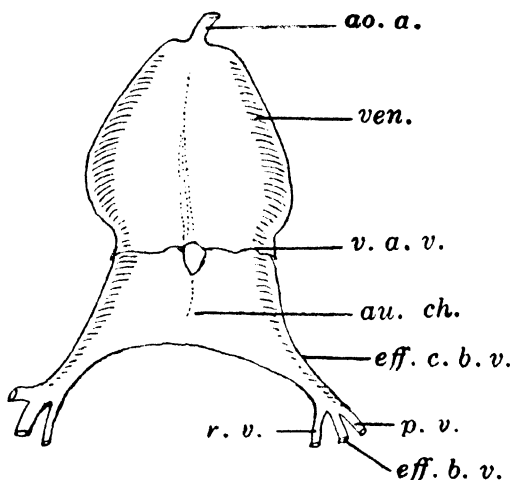


Fig. 29.— A diagram of the heart showing the roots of the principal blood-vessels. *ao. a.*, anterior aorta; *au. ch.*, inter-auricular channel; *eff. c. b. v.*, common efferent vein; *eff. b. v.*, branchial efferent veins; *p. v.*, pallial efferent vein; *r. v.*, renal vein; *v. a. v.*, auriculo-ventricular valve; *ven.*, ventricle. ($\times$ cir. 16)

ensuring apparently equal distribution of blood to the two aortae arising from the ventricle.

The *auricles*, which lie immediately behind the ventricle, are also incompletely divided into two, the left being slightly larger than the right. They are roughly triangular in shape, their narrow apices being continuations of the common efferent veins and their bases being joined on to the two divisions of the ventricle (fig. 29). The walls of the auricles are thin and non-papillate and are only slightly muscular; they are invested with a glandular epithelium containing a brown

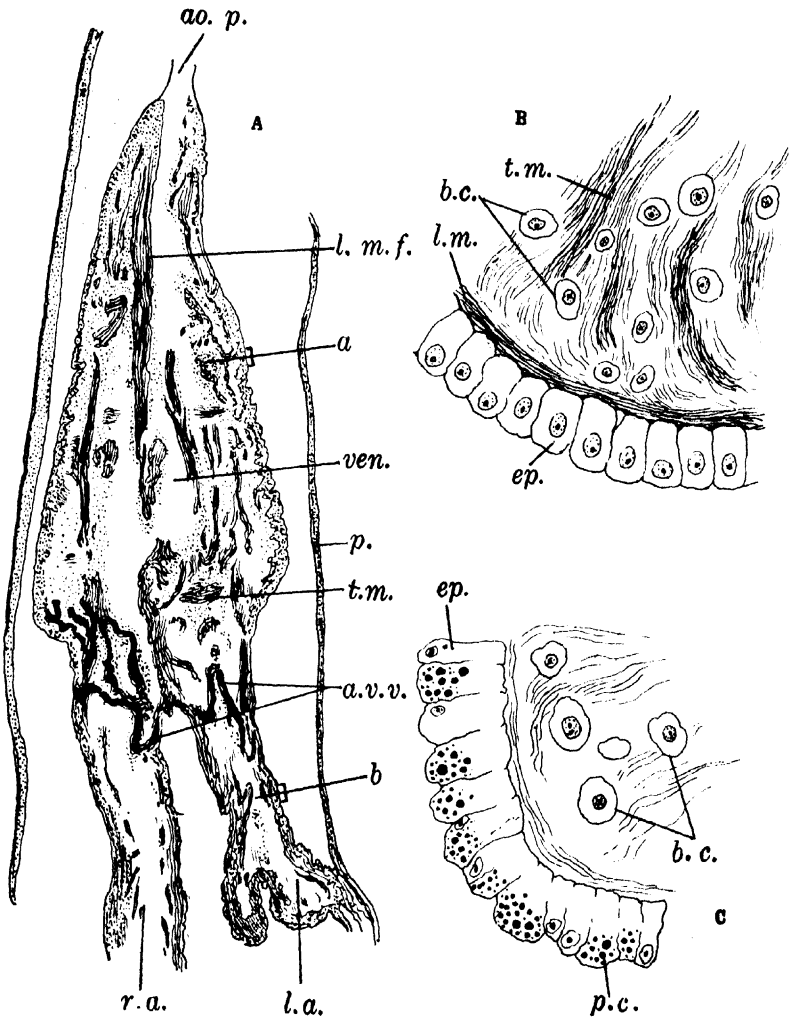


Fig. 30.— A. A longitudinal section of the heart taken at the level of the posterior aorta. B. A section across the wall of the ventricle taken at *a*. C. A section across the wall of the auricle taken at *b*. *ao. p.*, posterior aorta; *a. v. v.*, auriculo-ventricular valves; *b. c.*, blood-cells; *ep.*, epithelium covering the walls of the auricles and ventricle; *l. a.*, left auricle; *l. m.* and *l. m. f.*, longitudinal muscle-fibres; *p.*, wall of the pericardium; *p. c.*, pigment cells; *r. a.*, right auricle; *t. m.*, transverse muscle-fibres. (A., $\times$ cir. 20; B. & C., $\times$ cir. 900)

pigment (fig. 30 C), which gives the auricles a dark brown colour. The auricles open into the ventricle by two distinct auriculo-ventricular apertures which lie near each other and are guarded by a series of sphincter muscles (fig. 30 A), which act as valves preventing the reflux of blood into the auricles when the ventricle contracts. The auricles also communicate with each other ventrally through a broad transverse inter-auricular channel (fig. 29).

*The Arteries*¹.

The arteries are well-developed blood-vessels with stronger and thicker walls than those of the veins. The anterior aorta (fig. 31) emerges from the dorso-anterior corner of the ventricle (right chamber) and supplies blood to all the structures in the body except the adductor muscle. The posterior aorta takes its origin from the dorso-posterior corner of the ventricle (left chamber) and carries blood solely to the adductor muscle.

(a) THE ANTERIOR AORTA. The *anterior aorta* (fig. 31) runs forwards in a slightly zig-zag course, moving alternately to the right and left of the median axis of the body and, beyond the mouth, divides into two diverging branches known as the common pallial and circum-pallial arteries. All along its course, the aorta gives off branches which supply blood to the viscera of the body. The following are the main branches of the anterior aorta:

(1) The *rectal artery* arises close to the origin of the aorta and enters the rectum where it runs into the connective tissue of the typhlosole and continues its course right up to the extreme tip of the rectal papilla.

(2) The *reno-gonidial arteries* arise from the aorta near the junction of the œsophagus and the stomach and run towards the dorsal side of the body supplying blood chiefly to the nephridia and the gonads.

(3) The *visceral artery* arises ventrally along with the reno-gonidial artery and divides, soon after its origin, into two branches, one of which supplies blood to the sac of the crystalline style and the other gives off branches to the mid-gut, the nephridia and the gonads.

1. The description of the circulatory system is based on observations made on specimens, first injected with borax-carminé in 70 per cent. alcohol through the ventricle for the arteries and the common afferent vein for the veins, then fixed in 5 per cent. formalin, dehydrated and cleared in cedar wood oil.

(4) The *hepatic artery* arises from the aorta close to and in front of the visceral artery and divides into two branches, one supplying the digestive diverticulum and the other, the intestine and the gonads.

The visceral and hepatic arteries are large blood-vessels which drain away most of the blood from the anterior aorta.

(5) The *gastric arteries* arise immediately in front of the hepatic artery and consist of anterior and posterior gastric arteries. The *anterior gastric* is the larger of the two and supplies blood to the stomach, the digestive diverticula and the gonads, while the *posterior gastric* supplies only the stomach.

(6) The *cephalic artery* arises in front of the gastric arteries and supplies blood to the anterior cephalic region of the animal.

(7) The *labial artery* arises at the level of the labial palps and soon divides into several branches supplying blood to the right and left labial palps.

(8) The *common pallial arteries*. Beyond the mouth, the anterior aorta divides into two diverging branches, the *common pallial arteries*, which run towards the edges of the mantle and together form the *circum-pallial artery*. They supply blood to the mantle.

Besides the principal arteries enumerated above, there are several smaller blood-vessels which arise from the anterior aorta at intervals and supply blood to the general connective tissue of the body.

(b) THE POSTERIOR AORTA. The *posterior aorta* (fig. 31) is a large vessel which runs along the ventral surface of the rectum during the first part of its course and then travels downwards on the anterior side of the adductor groove. Finally, it enters the adductor muscle and divides into several branches which supply blood to the whole of this large muscle. It is interesting to note that the posterior aorta supplies blood exclusively to the adductor muscle and to no other organ of the body. Thus about one-half of the arterial blood from the heart is carried to this muscle.

The Veins.

The venous system consists of sinuses, afferent and efferent systems of veins, and the blood-vessels of the gills.

The blood is carried from the sinuses into the afferent

veins which ultimately break up into the gills. From the gills, the branches of the efferent veins convey the blood to the auricles of the heart.

(a) THE SINUSES. The sinuses are irregular blood-

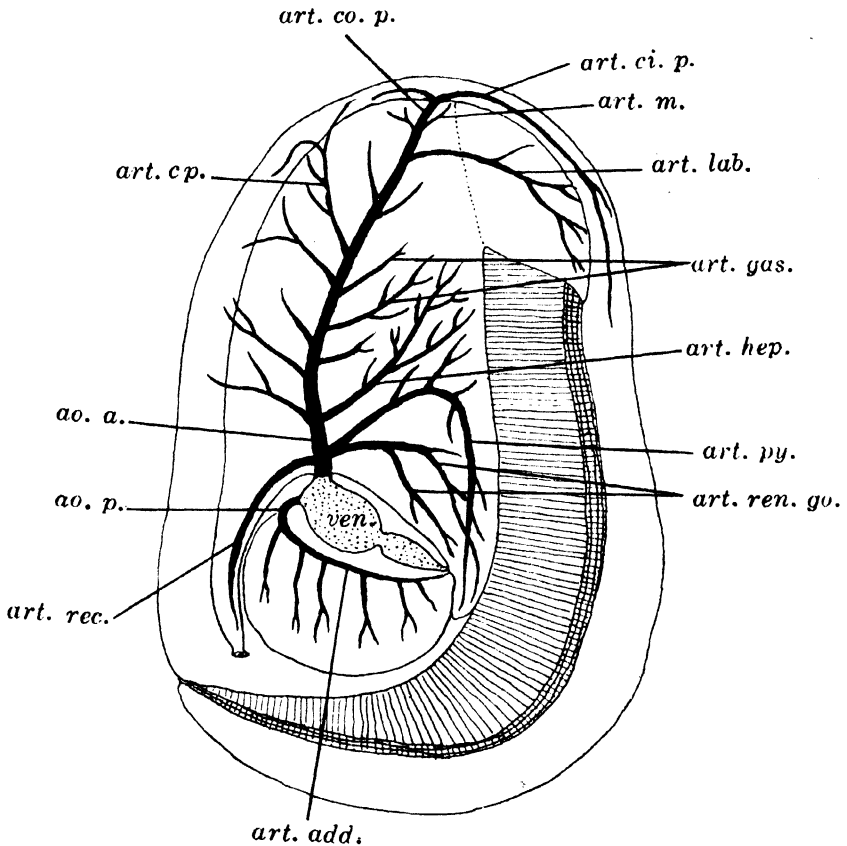


Fig. 31.— The arterial system as seen from the right side. *ao. a.*, anterior aorta; *ao. p.*, posterior aorta; *art. add.*, adductor artery; *art. cp.*, cephalic artery; *art. ci. p.*, circum-pallial artery; *art. co. p.*, common pallial artery; *art. gas.*, gastric artery; *art. hep.*, hepatic artery; *art. lab.*, labial artery; *art. m.*, mouth artery; *art. py.*, visceral artery; *art. ren. go.*, reno-gonidial arteries; *ven.*, ventricle.

spaces, into which the arteries open and from which the veins carry all the blood to the common afferent vein. The

sinuses, therefore, take the place of capillaries, between the arteries on the one hand and the veins on the other. There are three main sinuses in the body of the oyster:

1. The *visceral sinus* is very irregular in its outline and penetrates the entire visceral mass. Its blood is drained into the common afferent vein through the hepatic, renogonidial and other veins (fig. 32).

2. The *renal sinus* is made up of two kinds of sinuses: sinuses of the first kind surround the main nephridial structures and open into the efferent branchial vessels at regular intervals. Sinuses of the second kind (fig. 32) are situated on the posterior side of the body between the adductor muscle and the heart. They are smaller in extent than the visceral sinus and surround the spongy tissue connected with the inter-nephridial passage. A single large vein, the *renal vein*, carries the blood from this sinus into the common afferent vein.

3. The *muscle sinus* (fig. 33) is the smallest of the three sinuses. It is situated on the left side of the animal almost exactly below the renal sinus, on the ventral surface of the adductor muscle, facing the pyloric region. A single *muscle vein* carries blood from this sinus into the common afferent vein.

(b) THE AFFERENT VEINS. The system of afferent veins consists of the common afferent and a pair of lateral afferents and their branches.

1. The *common afferent vein*. The common afferent vein (figs. 8 and 32) is an unpaired vessel running along the line where the ends of the inner ascending lamellæ of the inner demibranchs of both gills are fused with each other and also with the visceral mass. It runs throughout the whole length of the gills—from the bases of the labial palps to the extreme posterior end. It is a vein without any epithelial lining. In dissections, the common afferent is seen to be riddled with a double series of large and small apertures (fig. 8), lying on either side of the blood-vessel against the lamellar edges of each side. The larger holes are few and distantly spaced; they open into the inter-lamellar bars which run across the floor of the supra-branchial chamber, and carry blood to the transverse veins, which in their turn open into the lateral afferent veins (fig. 33). The smaller holes are many and are placed quite near each other; they open into the

vessels of the inter-lamellar septa or junctions which come up to the level of the gill-bases (fig. 8).

In the first half or two-thirds of its course, *i. e.* as far as the gills are attached to the visceral mass, the common afferent vein receives blood from the body (fig. 32) and at the same time distributes it to the gills through channels in the inter-lamellar junctions and the inter-lamellar bars. But in its

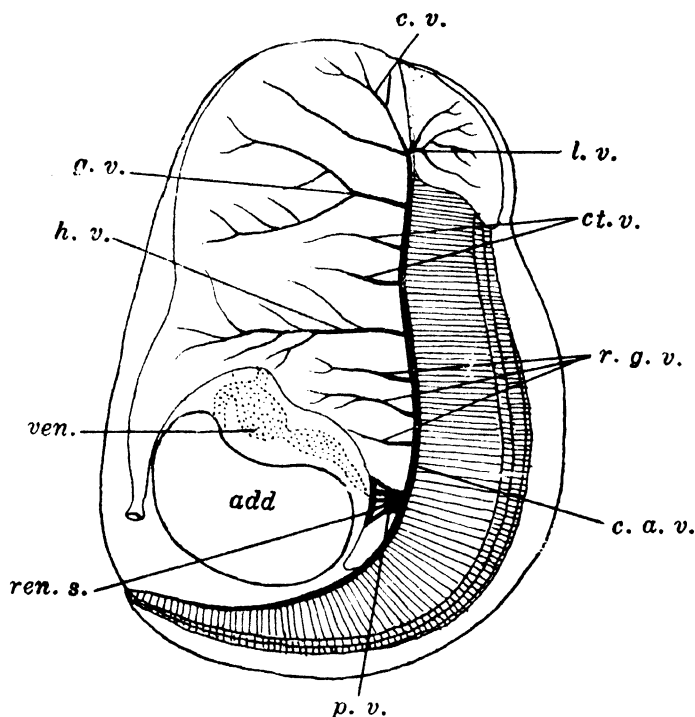


Fig. 32.— Venous system viewed from the right side. *add.*, adductor muscle; *c. v.*, cephalic vein; *c. a. v.*, common afferent vein; *ct. v.*, veins from connective tissue; *g. v.*, gastric vein; *h. v.*, hepatic vein; *l. v.*, labial vein; *p. v.*, renal vein; *ren. s.*, renal sinus; *r. g. v.*, reno-gonidial veins; *ven.*, ventricle.

last part, *i. e.*, in the region where the gills are free from the visceral mass, the common afferent vein does not receive any blood at all, but merely distributes blood to the gills.

The following are some of the important veins (fig. 32), which flow into the common afferent vein:

- (1) The *cephalic veins* collect blood from the cephalic

region of the oyster and join the common afferent immediately posterior to the point of entrance of the labial veins.

(2) The *labial veins* begin as a number of small vessels in the region of the labial palps, which open into larger vessels that ultimately join the common afferent vein at the base of the labial palps.

(3) The *gastric vein* is short and has many small branches. It runs almost parallel to the hepatic vein.

(4) The *hepatic vein* is the biggest vein, with the possible exception of the renal. Many small veins arise from the visceral sinus and join together to form the large hepatic vein.

(5) The *reno-gonidial veins* consist of many vessels forming a network in the reno-gonidial mass of the body. Each small vein in this area opens separately into the common afferent vein. In a series of transverse sections of the body of the animal at this level, openings of many veins into the common afferent vein are clearly seen.

(6) The *renal vein*. Next to the hepatic, the renal is the largest vein in the body but has a very short course. It takes its origin from the renal sinus and flows straight into the common afferent vein. No branches are seen to enter the renal vein.

(7) The *muscle vein*. All the veins mentioned above are clearly seen from the right side of the animal, but the muscle vein is only visible from the left side. It is short and narrow and arises from the muscle sinus into which the arteries of the adductor muscle open. The muscle vein runs straight across, above the pyloric region, into the common afferent vein.

2. The *lateral afferent veins*. The lateral afferent veins (fig. 33) are paired. Each of them runs along the base of the outer ascending lamella of the outer demi-branch of a gill, which is fused with the mid-portion of the mantle lobe (fig. 10, *a.b.v.*). These veins like the common afferent, run along the whole length of the gills.

The lateral afferent veins also have no epithelial lining. In dissections, they show a series of openings, some of them larger than others. The smaller openings are situated on the inner walls away from the mantle, while the others are found on both walls and are really the openings of the posterior pallial and transverse veins into the lateral afferents.

The following are the principal veins (fig. 33) opening into the lateral afferent veins:

(1) The *anterior pallial veins* (fig. 34, *a. d. v.*, *a. v. v.*) are a pair of vessels starting from the anterior pallial region and opening into the lateral afferent veins at the bases of the labial palps.

(2) The *posterior pallial veins* (fig. 34, *p. d. v.*, *p. v. v.*) are of two kinds: some of them carry blood directly to the auricles,

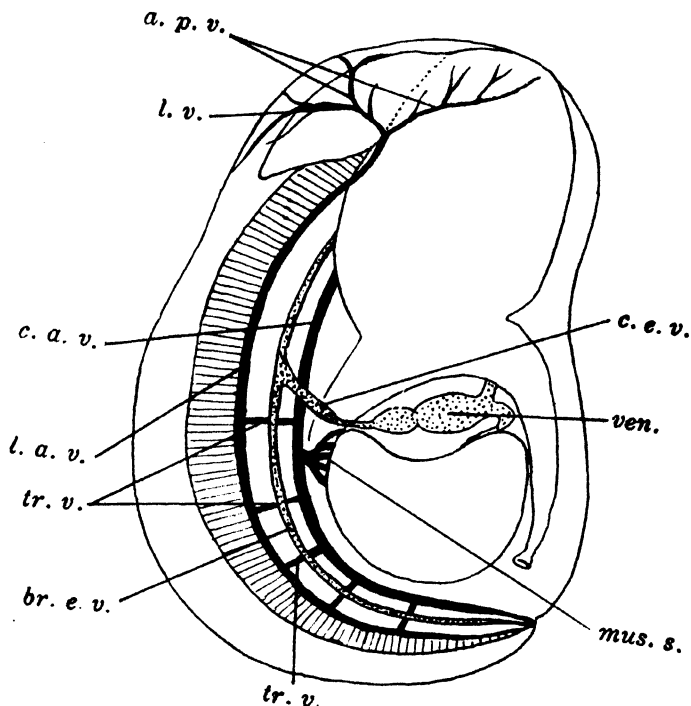


Fig. 33.— Venous system viewed from the left side. *a. p. v.*, anterior pallial veins; *br. e. v.*, branchial efferent vein; *c. a. v.*, common afferent vein; *c. e. v.*, common efferent vein; *l. a. v.*, lateral afferent vein; *l. v.*, labial vein; *mus. s.*, muscle sinus; *tr. v.*, transverse veins; *ven.*, ventricle.

while others open into the lateral afferent veins of both sides at short intervals along the line of concrescence of the mid-portion of the mantle with the gills.

(3) The *transverse veins* (fig. 10) pass through interlamellar bars running across the floor of the supra-branchial

chamber at long or short intervals. These veins bring a certain quantity of blood from the common afferent to the lateral vein.

(c) BLOOD-VESSELS IN THE GILLS. Before the blood returns to the auricles through the efferent veins, it passes through the gills and is thoroughly aerated. The blood-vessels in the gills run through the inter-lamellar and inter-filamentar junctions.

From the afferent veins, the blood flows into: (1) The *inter-lamellar vessels* lying in the inter-lamellar septa through the apertures already mentioned. These vessels give off branches during their course towards the ventral edges of the gills. Each branch runs into a narrow vessel which is closely apposed to the principal filament of each fold. (2) The narrow vessels of the principal filaments give off branches in their turn, which run through the inter-filamentar junctions and become the *inter-filamentar vessels*.

In the descending lamellæ of each gill, the blood flows from the inter-filamentar into the inter-lamellar vessels through the narrow vessels of the principal filaments. From the inter-lamellar vessels it runs into the efferent veins of which there is one in each axis of the gill (fig. 8).

(d) THE EFFERENT VEINS. The system of efferent veins consists of the branchial efferents and the pallial efferents, all of which finally open into the common efferent veins.

The *common efferent veins* are very short and paired. Each of them opens immediately after its formation into the auricle through the elongated posterior portion of the latter (fig. 29). It is formed by the following efferent veins:

(1) The *branchial efferent veins* are paired. Each of them runs along the axis of the gill beneath the branchial nerve (fig. 10). During its course through the visceral mass each branchial efferent runs along the inner border of the nephridial tube and crosses over the latter to open into the auricle. Within the visceral mass, renal sinuses of the second kind open into the branchial efferents at more or less regular intervals. In dissections along the axis of the gills, a paired series of apertures of almost uniform size can be seen along both the walls of the branchial efferent veins (fig. 8).

(2) The *pallial efferent veins*. The blood circulating in the posterior part of the mantle through the circum-pallial artery is carried back to the common efferent veins through the pallial efferents. Part of the blood from this region

of the mantle, however, goes to the gills, while the rest is taken to the auricles through these veins. These run parallel to the line of concrescence of this part of the mantle with the gills. At the extreme anterior end of the supra-branchial chamber, each of them joins the common efferent vein immediately before the latter enters the auricle.

From the foregoing description, it will be clear that

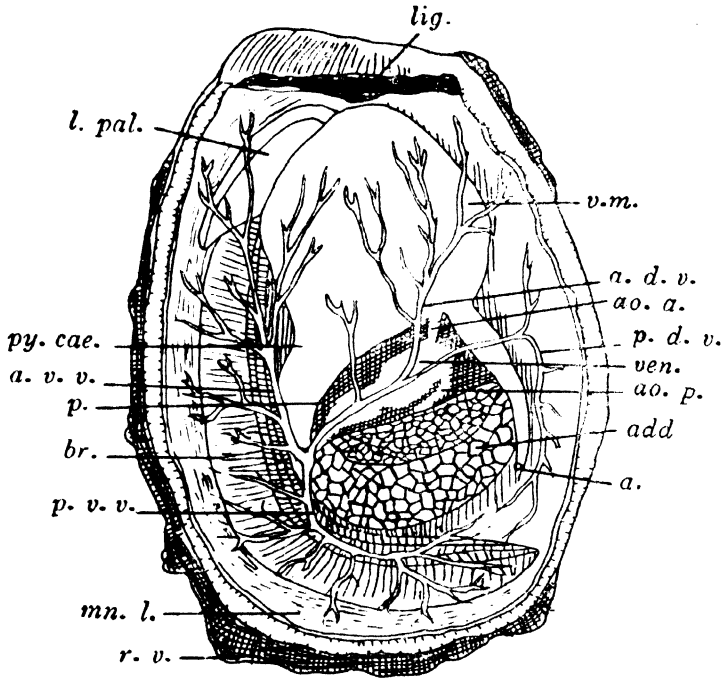
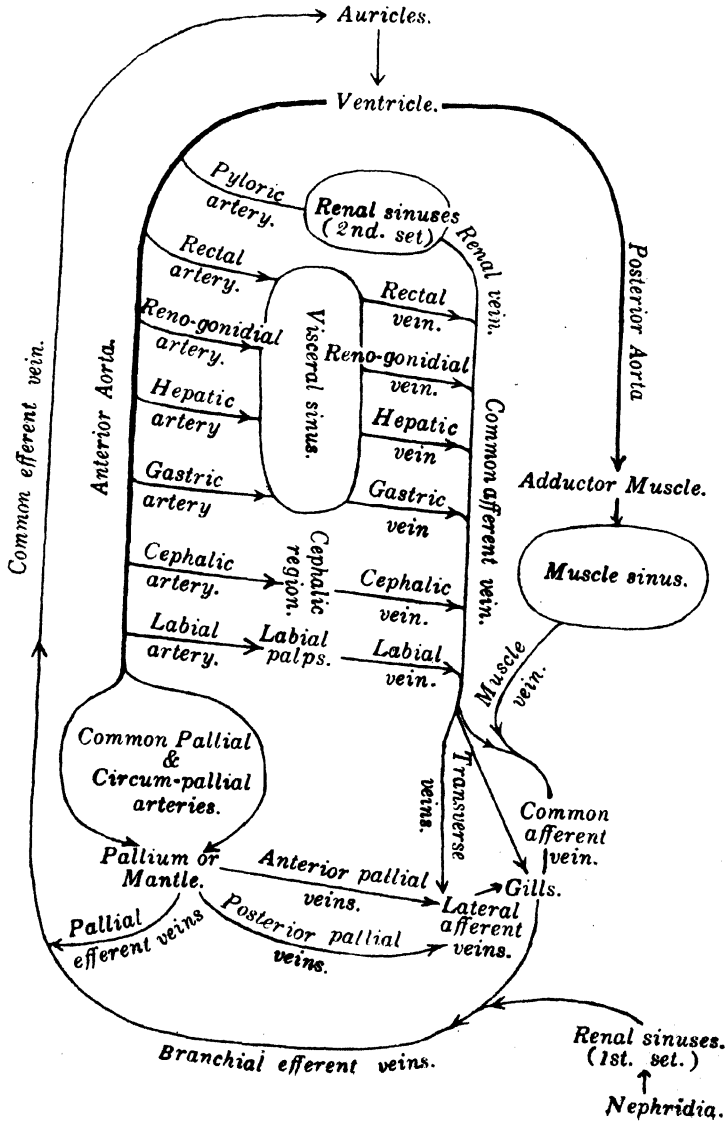


Fig. 34.— Diagram of the veins in the mantle. *a.*, anus; *add.*, adductor muscle; *a. d. v.*, anterior dorsal vein; *ao. a.*, anterior aorta; *ao. p.*, posterior aorta; *a. v. v.*, anterior ventral vein; *br.*, gill; *l. pal.*, labial palp; *lig.*, hinge-ligament; *mn. l.*, mantle-lobe; *p.*, pericardium; *p. d. v.*, posterior dorsal vein; *p. v. v.*, posterior ventral vein; *py. cae.*, pyloric caecum; *r. v.*, right valve of the shell; *v. m.*, visceral mass; *ven.*, ventricle.

almost all the venous blood, whether coming from the sinuses or directly from the tissues, ultimately passes either into the common afferent vein or into the lateral afferent veins. Since these veins run along the basal edges of the gills, the blood must be conveyed to the exposed surfaces of the gills for

aëration. This is accomplished by the passage of blood in the gills through the inter-lamellar and inter-filamentar vessels.

The complete circulation of the blood can be easily followed from the following diagram:



THE NERVOUS SYSTEM

The nervous system of the oyster is comparatively simple and consists of two pairs of ganglia, the *cerebral* and the *visceral*, which send out nerves to the different parts of the body. The *pedal ganglia* of other Lamellibranchs are wanting in this type owing to the absence of the foot.

The *cerebral ganglion* of each side lies imbedded in the loose connective tissue between the bases of the labial palps. The two ganglia are widely separated from each other and are slightly asymmetrical in position—the left ganglion lying at the lower end of the base of the inner labial palp, and the right slightly above and to the right of the outer labial palp of its side. A *cerebral commissure* passing dorsally over the posterior end of the œsophagus connects the two cerebral ganglia. The commissure forms a long inverted U-shaped loop (fig. 35) on account of the long distance between the cerebral ganglia and the œsophagus.

Each cerebral ganglion gives off anteriorly a *common pallial nerve* and a small *labial nerve*. The *common pallial nerve*, after its origin, traverses the connective tissue of the labial palps and then enters the mantle-lobe of its side at the level of the mouth. There it divides into two branches, which pass on to the margin of the mantle to join the *circum-pallial nerve*. The *labial nerve* soon after its origin bifurcates to supply nerve-branches to the labial palps.

There being no otocyst in *O. cucullata*, there is no trace of an *otocystic nerve*. Similarly, there being no pedal ganglia, *cerebro-pedal connectives* are absent.

The *visceral* or the *parieto-splanchnic ganglia* (figs. 35 and 36) lie in a slight depression on the antero-ventral surface of the adductor muscle close to the ventral end of the pyloric region. The two ganglia are fused to form one large mass, in which two separate parts cannot be distinguished except in sections. The ganglia are covered over by a single layer of epithelium and together form the largest ganglionic mass in the body giving origin to most of the nerves of the animal. This great development of the visceral ganglia as compared with the cerebral is due to the fact that the sense-organs and the muscles are best developed in the posterior part of the body—the cephalic region being more or less vestigial.

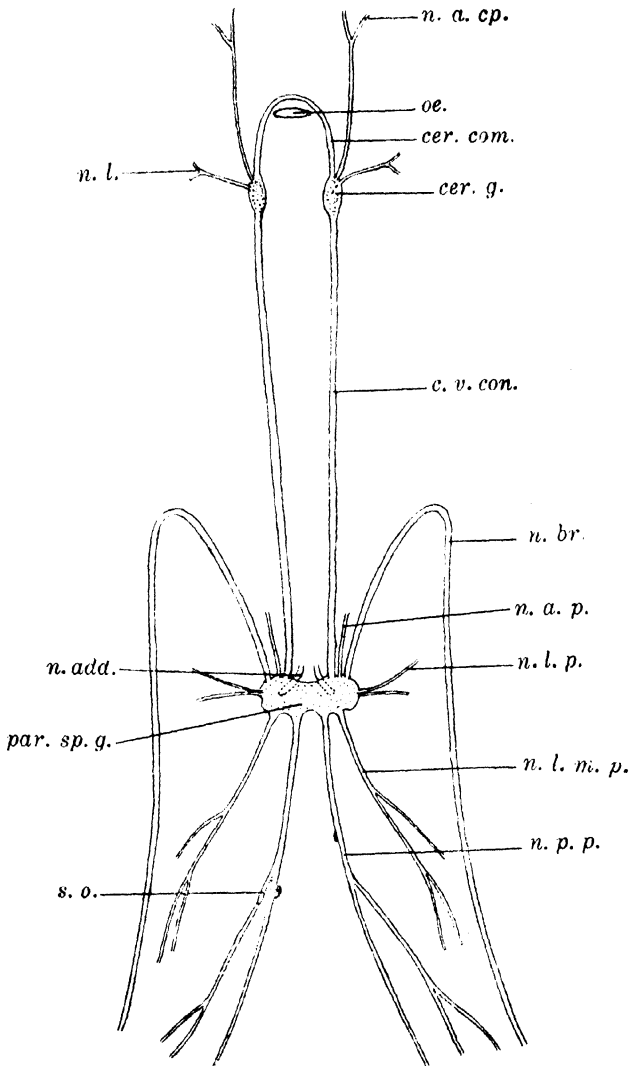


Fig. 35.— The nervous system. *cer. g.*, cerebral ganglion; *cer. com.*, cerebral commissure; *c. v. con.*, cerebro-visceral connective; *n. a. cp.*, common pallial nerve; *n. a. p.*, anterior pallial nerve; *n. add.*, adductor nerve; *n. br.*, branchial nerve; *n. l.*, labial nerve; *n. l. p.*, lateral pallial nerve; *n. l. m. p.*, latero-median pallial nerve; *n. p. p.*, posterior pallial nerves; *oe.*, oesophagus; *par. sp. g.*, parieto-splanchnic ganglia; *s. o.*, sense-organ.

The visceral ganglia are connected with the cerebral by means of the *cerebro-visceral connectives* (fig. 35), which lie buried in the connective tissue of the digestive diverticulum, the gonads and the renal organs. Besides these connectives, the visceral ganglia give off *six* pairs of nerves (fig. 36) innervating the organs surrounding them: (1) the branchial nerves, (2) the adductor nerves, (3) the anterior pallial nerves, (4) the lateral pallial nerves, (5) the latero-median pallial nerves, and (6) the posterior common pallial nerves.

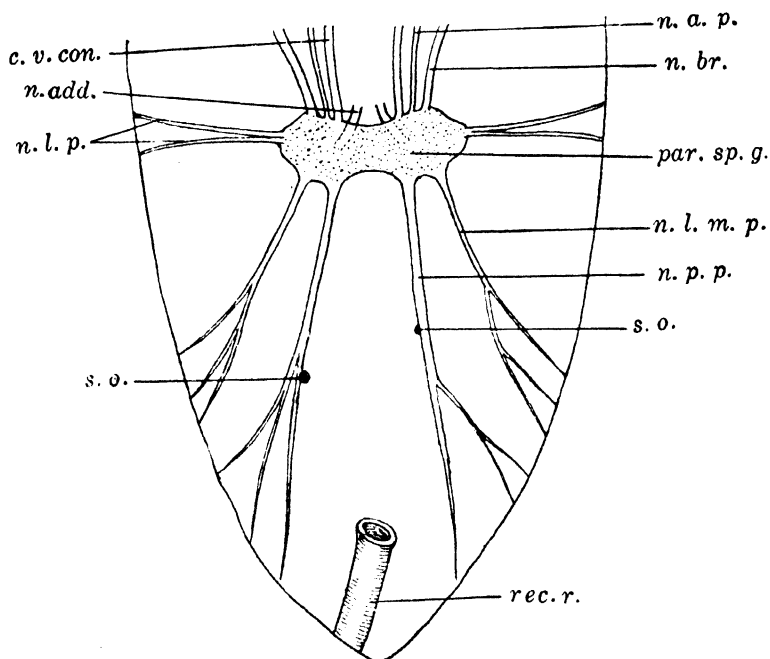


Fig. 36.— The visceral ganglia and the nerves given off from them. *c. v. con.*, cerebro-visceral connective; *n. add.*, adductor nerve; *n. a. p.*, anterior pallial nerve; *n. br.*, branchial nerve; *n. l. p.*, lateral pallial nerve; *n. l. m. p.*, latero-median pallial nerve; *n. p. p.*, posterior pallial nerve; *par. sp. g.*, parieto-splanchnic ganglia; *rec. r.*, rectal ridge; *s. o.*, sense-organ. ($\times$ cir. $2\frac{1}{2}$)

nerves, (4) the lateral pallial nerves, (5) the latero-median pallial nerves, and (6) the posterior common pallial nerves.

The *branchial nerves* arise from the visceral ganglia close to the origin of the cerebro-visceral connectives and run forwards parallel to them for a short distance. During their

course, they traverse the renal organs on each side of the pyloric region and then sharply turn backwards where the efferent blood-vessels enter the gill-axis. Here the nerves pass into the branchiæ and travel to their extremities. In the substance of the gills, these nerves run parallel to the efferent branchial vessels (figs. 9 and 10), and give off branches during their course to the gill-filaments.

In *Placuna placenta* and the pearl oyster, the branchial nerves enter the ctenidial axis immediately after leaving the visceral ganglia.

The large *adductor nerves* (fig. 36) arise on either side of the visceral ganglia from their dorsal surface and supply the whole mass of the adductor muscle.

The pallium is innervated from the visceral ganglia by means of *four* pairs of nerves (figs. 36 and 37). The *anterior pallial nerves* are stout cords which take their origin from the visceral ganglia slightly dorsal to the place of origin of the cerebro-visceral connectives. They pass through the nephridia on both sides and run forwards over the wall of the pericardium to the dorsal side of the body. Each nerve gives off many small branches to the central part of the mantle close to the rectum and then breaks up into small nervules innervating practically the whole of the dorsal side of the mantle. The *lateral pallial nerves* take their origin from the two sides of the visceral ganglia and each of them immediately divides into two strong nerves which run forwards and outwards to supply the anterior ventral side of the pallium. In the pallium, these nerves divide and sub-divide to form a network of delicate nervules which finally end in the pallial margin.

The *lateral median pallial nerves* pass backwards and outwards, each of them dividing into two branches. The outer passes at once into the mantle while the inner runs backwards and divides into smaller branches which enter the pallium to join the circum-pallial nerve. The *posterior common pallial nerves* are stout nerves which emerge from the posterior end of the visceral ganglia and pass straight into the sheath of the adductor muscle on its ventral side as far as the region of the rectum. Later they come out to enter the mantle, where they divide into several branches.

The *circum-pallial nerve* runs parallel to the free thickened pallial margin just close to the pallial artery. It is a thick nerve with a double origin. Anteriorly it is connected with the cerebral ganglia through the anterior

pallial nerves and posteriorly with the visceral ganglia through the posterior pallial nerves. Ganglion cells occur throughout its whole extent. Branches are given off from this nerve to the margin of the mantle.

Fig. 35 is a representation of the entire nervous system while fig. 37 shows the principal branches of the pallial nerves given off from the visceral ganglia to the

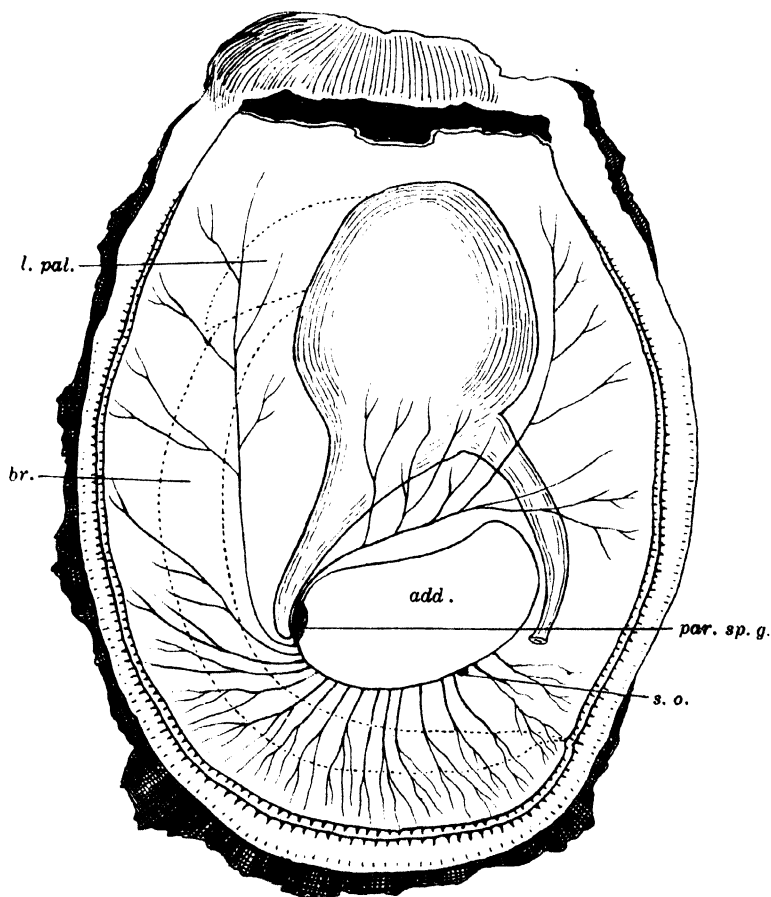


Fig. 37.— The pallial nerves given off from the visceral ganglia. The nerve with its branches on the right side of the diagram is the *anterior pallial nerve*, the nerve with its branches towards the lower end of the figure is the *posterior common pallial nerve*, and the nerve on the left side is the *lateral pallial nerve*. *add.*, adductor muscle; *br.*, position of the branchiae; *l. pal.*, position of the labial palps; *par. sp. g.*, visceral ganglia; *s. o.*, sense-organ. ($\times$ cir. 24)

mantle. It will be observed that the mantle has a double nerve-supply, receiving nerves both from the cerebral and the visceral ganglia. This is probably due to the fact that sense-organs and important muscles are found in the pallium.

THE SENSE-ORGANS

Owing to its sedentary habit of life, the sense-organs of *Ostrea cucullata* are degenerate so that the otocyst and the osphradium of other molluscs are absent. The only sensory structures found are: (1) the sensory epithelial cells, and (2) the abdominal or pallial sense-organs.

The *sensory epithelial cells* are found singly or in groups all over the general surface of the body but are most numerous on the apices of the pallial tentacles (s. c., fig. 7), the edges of the mantle-lobes, the labial palps and the outer epithelium surrounding the rectal papilla. In shape and size, these sensory cells differ but slightly from the ordinary epithelial cells of the mantle. Each cell is rather elongated with the nucleus at the base and a bundle of long delicate sense hairs at its free end. These cells are probably tactile in function.

The *abdominal or pallial sense-organs* (fig. 36) are paired, the right sense-organ being larger than the left. They are situated on the edge of the mantle, one on each side of the supra-branchial chamber, distinctly marked off from the surrounding area. The right sense-organ is visible with the naked eye while the left is very small and can be made out only with the help of a lens.

In sections, a sense-organ is a very prominent structure and appears as a characteristic protuberance. Fig. 38 represents a section passing through a sense-organ, while fig. 39 shows the cells at the tip of the sense-organ very highly magnified. Two kinds of cells can be distinguished in the sense-organ: (1) the long *epithelial cells* with oval or rounded nuclei lying near the centre of each cell, and (2) the *neuro-epithelial cells* having elliptical nuclei and connected with nerve-fibres. There is a distinct layer of cuticle covering the free surface of both kinds of cells. The basal membrane is pierced by branches of the posterior pallial nerves which run immediately beneath the epithelial cells (figs. 38 and 39). These nerve-fibrils enter the neuro-epithelial cells and break up into finer processes within the cells. Both kinds of cells composing the sense-organ are longer than the ordinary

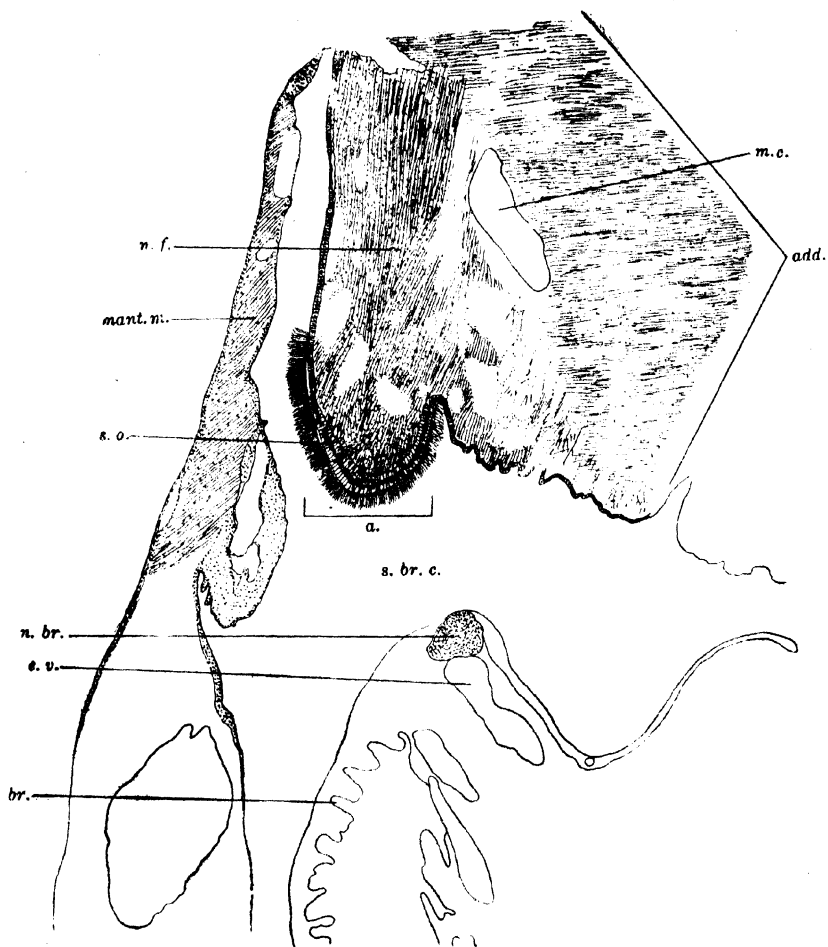


Fig. 38.— A transverse section passing through the pallial sense-organ. *a.*, the tip of the sense-organ, shown still further magnified in fig. 59; *add.*, adductor muscle; *br.*, branchiae; *e. v.*, efferent vessel; *m. c.*, a split in the adductor muscle; *mant. m.*, mantle with muscles; *n. br.*, brachial nerve; *n. f.*, nerve fibres; *s. o.*, sense-organ; *s. br. c.*, supra-branchial chamber. ($\times$ cir. 70)

epithelial cells and are quite distinctive. They bear very long and wavy sense-hairs (fig. 39).

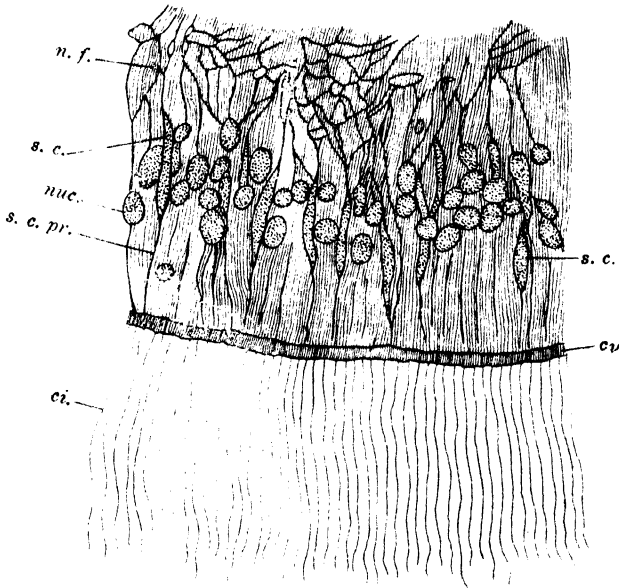


Fig. 39.— The tip of the sense-organ highly magnified. *ci*, cilia with sense-hairs; *cu.*, cuticle; *n. f.*, nerve fibrils; *nuc.*, nucleus of the epithelial cell; *s. c.*, sensory cell with its nucleus; *s. c. pr.*, sensory cell process. ($\times$ cir. 600)

THE EXCRETORY SYSTEM

The excretory system of the Bombay oyster consists of a pair of nephridia situated on either side of the visceral mass. They lie for the greater part between the efferent branchial vessel and the ventral margin of the pericardium (fig. 4). Morphologically, the nephridia are true coelomoducts, since they open, at one end, directly to the exterior and at the other, through the reno-pericardial canals (fig. 40) into the pericardium, which is really a part of a true coelom.

Fig. 40 shows the two nephridia in outline¹ lying one on each side of the pericardium and the heart. The nephridia are markedly asymmetrical, the right being larger than the left. This asymmetry is probably due to the fact that the visceral mass is more highly developed on the left than on the right and consequently there is more space for the right nephridium to spread out.

Each nephridium consists of a central portion, the *body*, with its short wide duct, and the *two limbs*, an anterior and a posterior. The body of the nephridium (fig. 40) is the widest portion enclosing a large lumen and communicating with the nephridium of the other side through a transverse *inter-nephridial passage* or *canal* (figs. 40 and 42). It tapers towards the anterior and posterior ends of the animal, giving rise to an *anterior* and a *posterior limb*. The anterior limb of each nephridium lies along the branchial efferent vein and gives off a large number of fine dendritic branches (fig. 4) towards the side of the visceral mass. On the right side, the anterior limb gives off a small *pericardial lobe* encircling the ventral part of the pericardium. The pericardial lobe gives off hardly any branches at all and is absent on the left side. The posterior limb runs along the ventral border of the adductor muscle extending on the right side beyond the level of the parieto-splanchnic ganglia.

In a dissection, the first excretory structure to be noticed is the elongated slit-like external aperture of the common reno-gonidial duct or vestibule (fig. 4). This aperture,

1. The gross outline of each nephridium, especially the right, can be easily made out by injections through the renal aperture in the reno-gonidial duct.

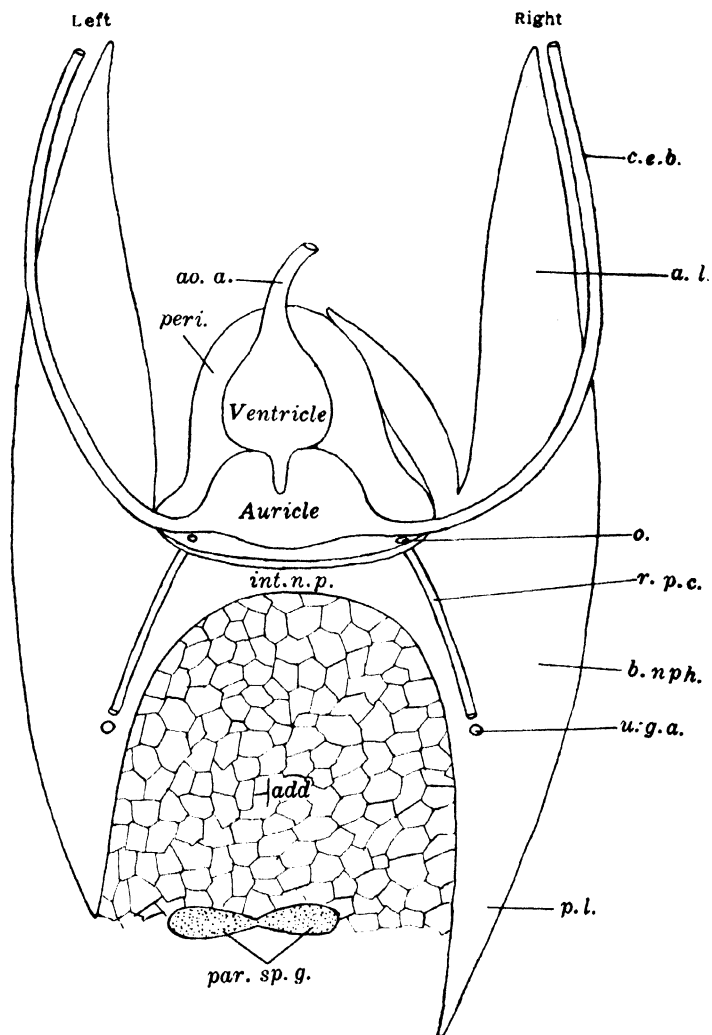


Fig. 40.—A diagrammatic representation of the nephridial system and its position in relation to the pericardium and the adductor muscle. *add.*, adductor muscle; *a. l.*, anterior limb of the right nephridium; *ao. a.*, anterior aorta; *b. neph.*, body of the nephridium; *c. e. b.*, common efferent vein; *int. n. p.*, inter-nephridial passage; *o.*, opening of the reno-pericardial canal into the pericardium; *p. l.*, posterior limb of the right nephridium; the *pericardial lobe* given off from the anterior limb of the right nephridium and lying next to the pericardium is shown in the diagram but has not been labelled; *par. sp. g.*, visceral ganglia; *peri.*, pericardium; *r. p. c.*, reno-pericardial canal; *u. g. a.*, reno-gonidial aperture,

enclosed by two prominent lips, is surrounded by a pigmented brownish area near the antero-ventral margin of the adductor muscle where it can be easily distinguished from the surrounding whitish or cream-coloured tissue of the visceral mass. The nephridium of each side and the adjacent gonidial organ open through separate apertures into the vestibule. Both the excretory and genital products are, therefore, discharged into the vestibule whence they make their exit to the supra-branchial chamber through the external *reno-gonidial aperture*¹ (figs. 40 and 43).

Each nephridium (fig. 41) is essentially a hollow glandular tube leading from the renal aperture in the vestibule to a point near the entrance of the efferent branchial vessel into the visceral mass. The nephridial tube, especially its anterior limb, gives off branches all along its course, more on one side than on the other; these branches in their turn divide and re-divide, thus producing a fine much-branched arborescent structure (fig. 4) embedded in a loose connective tissue containing bundles of circular and longitudinal muscle-fibres.

Besides opening to the exterior through the renal aperture, each nephridium communicates with its fellow of the opposite side through the *inter-nephridial canal*, and with the pericardial cavity through a *reno-pericardial canal* (fig. 41). The inter-nephridial canal runs along the ventro-posterior margin of the pericardium between it and the adductor muscle. It is formed by a fusion of two tubes, each arising at right angles to the nephridia. Along its postero-ventral border, the canal gives off a number of tubules which anastomose with one another forming a kind of spongy tissue which extends through the visceral mass even into the fibres of the adductor muscle. The *reno-pericardial canals* (figs. 40 and 41) arise just a little posterior to the point of entrance of the efferent vessels into the auricles. Each canal begins in the pericardium with a wide funnel-shaped mouth, lined by the pericardial epithelium, and soon narrows down into a tube which opens into the distal end of the nephridium before the latter opens to the exterior (fig. 41). Each reno-pericardial canal starts almost at right angles to the body of the

1. In *Placuna placenta* and *Pecten*, there are no separate renal and genital openings but the genital products—the ova and the sperms—are shed into the cavities of the nephridia whence they make their exit through the renal pores along with the excretory products.

nephridium but runs parallel to it for the greater part of its course. The canal is ciliated throughout its length, the cilia varying in number both in the proximal and distal regions.

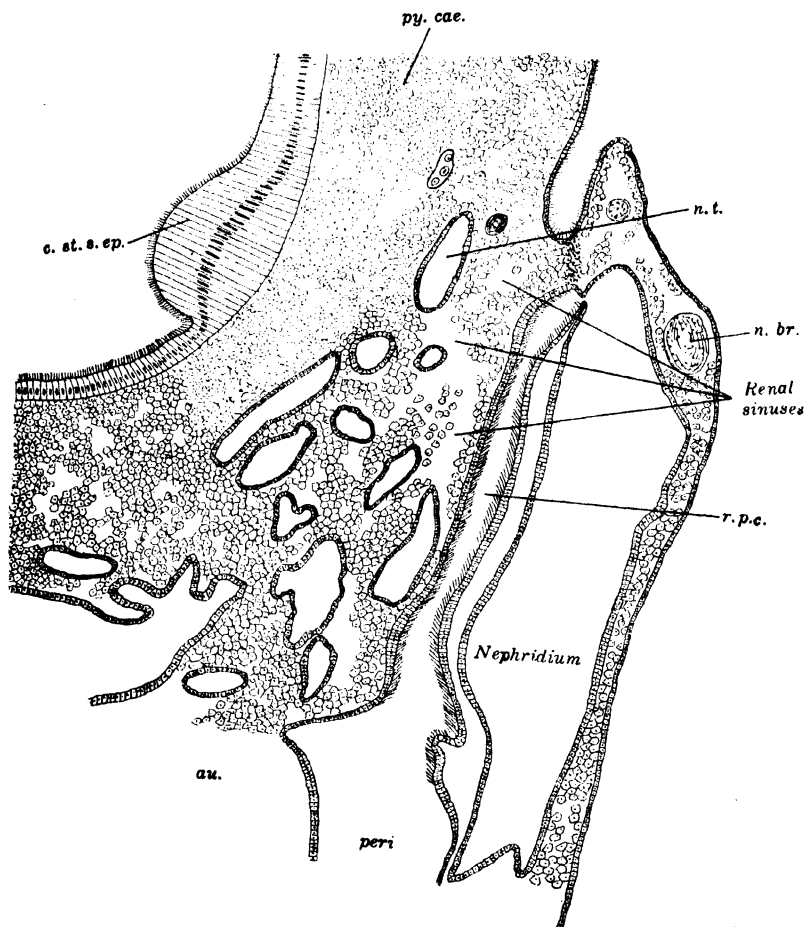


Fig. 41.—A section across a nephridium and the pyloric caecum. *au.*, auricle; *c. st. s. ep.*, epithelium of the crystalline style sac; *n. t.*, nephridial tubule; *n. br.*, branchial nerve; *peri.*, pericardium; *py. cae.*, pyloric caecum; *r. p. c.*, reno-pericardial canal; the ciliated pit at the right-hand top corner is the common reno-gonidial vestibule, immediately below it is the opening of the reno-pericardial canal into the nephridium; the renal sinuses shown in the diagram are of the second set (p. 82). ($\times$ cir. 42)

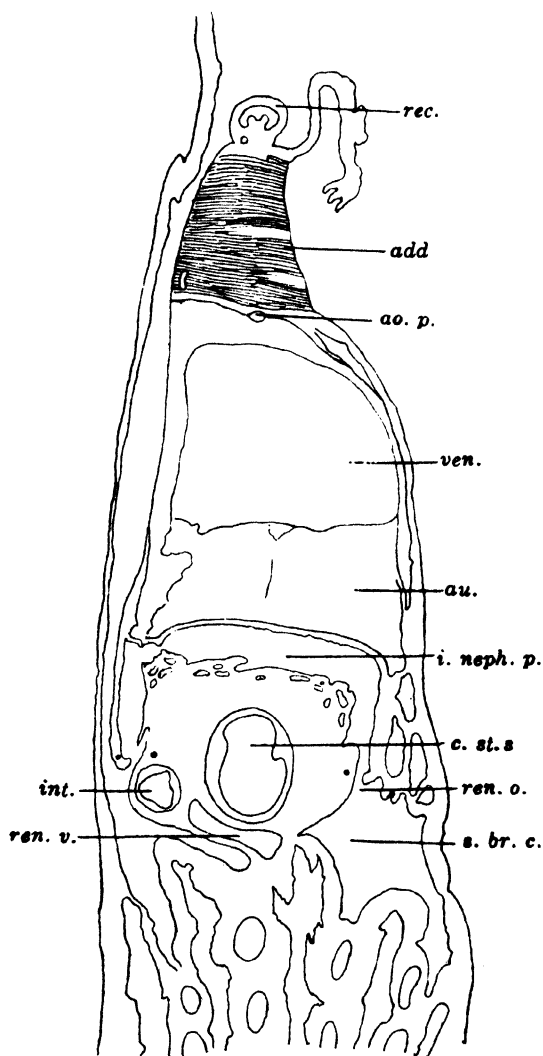


Fig. 42.—A section across the body of the oyster passing through the inter-nephridial passage and showing the renal opening into the supra-brachial chamber. *add.*, adductor muscle; *ao. p.*, posterior aorta; *au.*, auricle; *c. st. s.*, crystalline style sac; *i. neph. p.*, inter-nephridial passage; *int.*, intestine; *rec.*, rectum; *ren. o.*, renal opening; *ren. v.*, renal vein; *s. br. c.*, supra-brachial chamber; *ven.*, ventricle. ($\times$ cir. 14)

Besides the nephridia proper, there are other accessory excretory organs in the oyster. These consist of the so-called *pericardial glands* found on the auricles as well as on the inner walls of the pericardium. The excretions from these glands are drained off into the nephridium of each side through its reno-pericardial canal.

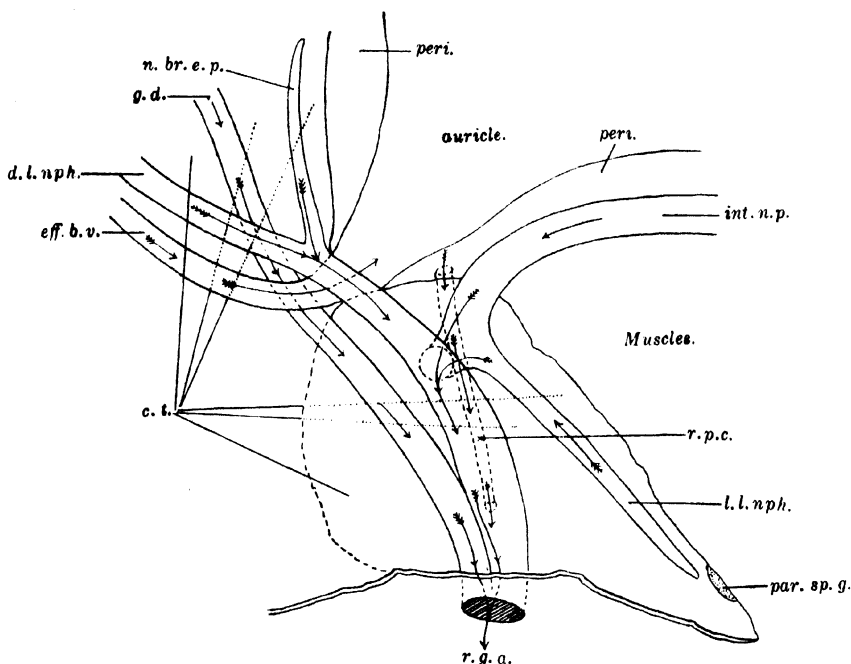


Fig. 43.—A diagrammatic representation of the right nephridium and its relations with other structures. *c. t.*, connective tissue; *d. l. nph.*, dorsal anterior limb of the nephridium; *eff. b. v.*, common efferent vein; *g. d.*, gonidial duct; *int. n. p.*, inter-nephridial passage; *l. l. nph.*, lower posterior limb of nephridium; *n. br. e. p.*, the pericardial lobe of the right nephridium encircling the pericardium; *par. sp. g.*, visceral ganglia; *peri.*, pericardium; *r. g. a.*, reno-gonidial aperture; *r. p. c.*, reno-pericardial canal.

The sinuses. All the nephridial structures except the reno-pericardial canal, are surrounded by a series of *sinuses* (fig. 41), which open into each other and hence appear to form one continuous structure. Two sets of sinuses can be distinguished according to their relation to the prominent blood-vessels. All those sinuses which surround the main nephridial structures and open into the efferent branchial vessels at regular intervals

form the first set. The second set includes those sinuses which surround the spongy tissue formed by the anastomosis of the tubules arising from the inter-nephridial passage. These sinuses open into one another and ultimately lead by a common vessel, the *renal vein* (fig. 42) into the afferent vein just before the latter leaves the visceral mass to enter the gills.

Histology of the excretory organs.

(a) *Nephridia.* The lumen of each nephridial tube or tubule is lined with a distinct epithelium which in its turn is surrounded by a basement membrane. The epithelium consists of glandular cells of three kinds (fig. 44): (1) The first kind of cells are small, cylindrical and vacuolated. They are found generally in the extreme anterior portion of the nephridial tubes and tubules. (2) The second variety consists of small cubical cells with indistinct vacuoles. The epithelium formed by these cells is in some places two or three cells deep and is supported by a sharply defined basement membrane. These cells line the tubules arising from the inter-nephridial passage. (3) Tall columnar cells with large prominent vacuoles form the third kind. These cells form the lining of the inter-nephridial passage, the nephridial tubes directly in contact with the efferent branchial vessels, as well as the distal portions of the nephridia just before they open into the reno-gonidial vestibule.

The tall columnar cells of the third kind are remarkable in appearance. They are about six to seven times as long as wide, are highly vacuolated near the surface and do not contain much stainable protoplasm. They have large rounded nuclei situated towards the base. The vacuoles are either empty or partially filled with a faintly staining fluid. The free surfaces of these cells are provided with delicate processes resembling cilia. Certain cells are found in the process of extrusion from the nephridial epithelium which seem to carry excretory matter along with them.

In the larger (right) nephridium, there is a clear vesicle seen at the junction of the reno-pericardial canal and the nephridium proper. The epithelium at this point is one cell thick and the cells are generally cubical with nuclei in the centre. There is no such structure in the other nephridium. The vesicle seems to open into the region of the renal opening. The basement membrane surrounding the epithelial lining of each nephridial tubule is bounded externally by bundles of circular and longitudinal muscle-fibres and the nuclei of the latter are clearly visible on the periphery.

(b) The *reno-pericardial canal*. The cavity of the reno-pericardial canal is lined throughout with a ciliated epithelium, the ciliated cells being more sparsely distributed in the proximal region than in the distal. In the latter, the cells are crowded and the cilia are dense and long. The epithelium of the funnel is a continuation of the pericardial epithelium round about that area and consists of ciliated cubical cells with nuclei

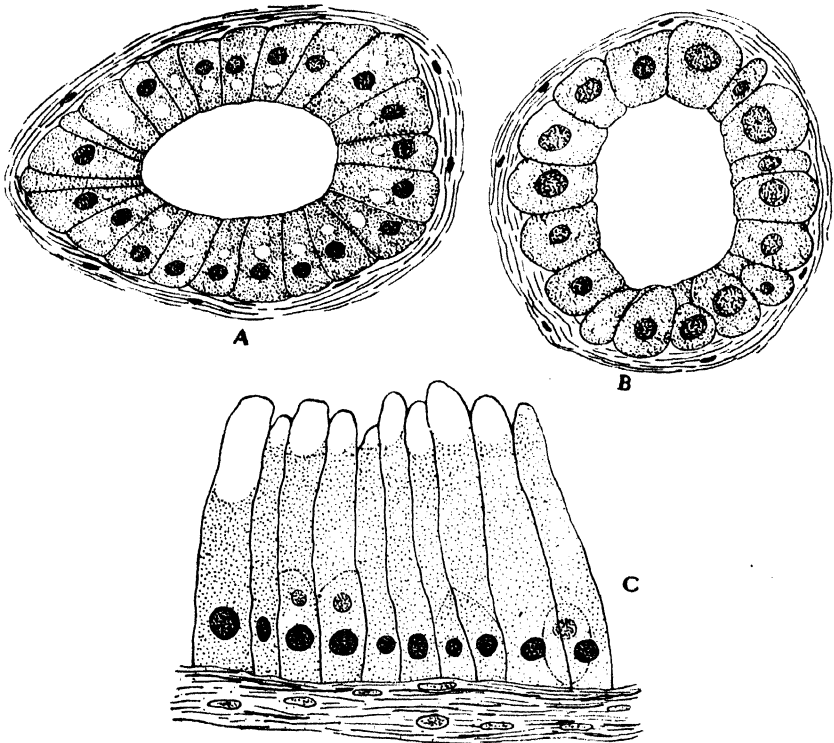


Fig. 44.— The three kinds of renal cells. A., the cylindrical vacuolated cells. B., small cubical cells. C., tall columnar cells. ($\times$ cir. 600)

in the centre. It is surrounded by a thin basement membrane and a few circular and longitudinal muscle-fibres. As the canal is traced towards the distal end, these epithelial cells become taller and the basement membrane forms a thicker sheath. This canal is not surrounded by any sinus.

Since the reno-pericardial canal opens into the most distal end of the nephridium before the latter runs into the reno-

genital duct (fig. 43), the region between the reno-pericardial opening into the nephridium and the nephridial opening into the reno-gonidial duct is lined by a mixed epithelium. Thus one side of the renal opening is glandular while the other side is ciliated like the reno-pericardial canal.

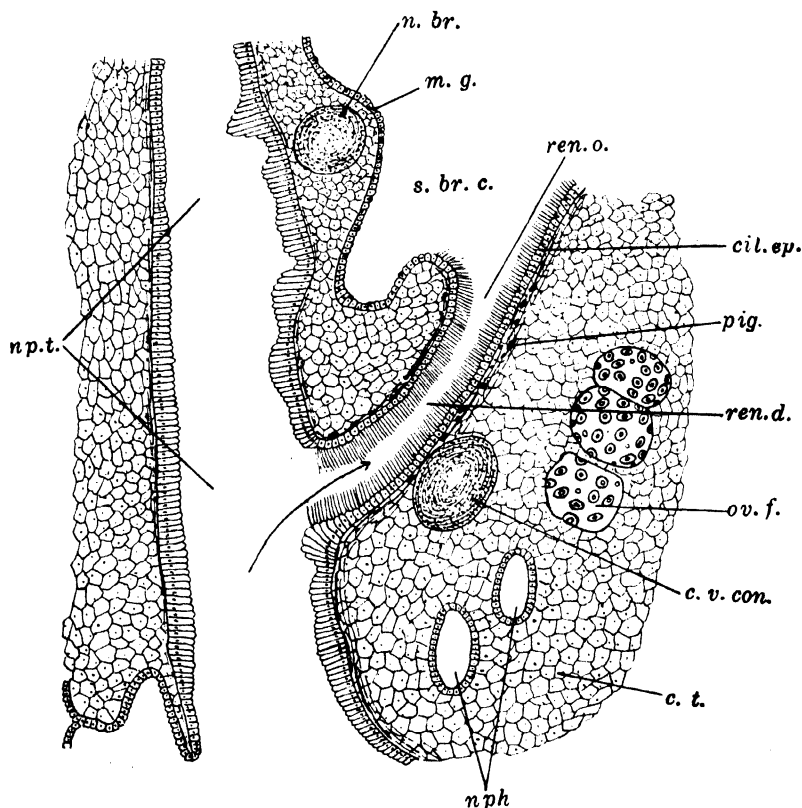


Fig. 45.—A section passing through the renal opening, the ovarian follicles and the nephridial tubules. *cil. e. p.*, ciliated epithelium of the renal duct; *c. t.*, connective tissue surrounding the nephridial tubules (*nph.*); *c. v. con.*, cerebro-visceral connective; *m. g.*, mucus gland cell; *np. t.*, main nephridial tube; *n. br.*, branchial nerve; *ov. f.*, ovarian follicles; *pig.*, pigment; *ren. d.*, renal duct; *ren. o.*, renal opening; *s. br. c.*, supra-branchial chamber. ($\times$ cir. 68)

(c) The reno-gonidial duct or vestibule. The reno-gonidial duct is lined all along with compact regularly arranged cilia. They are rather short and have small deeply staining granules at their bases. The external opening is guarded by two

prominent lips formed chiefly of muscle-fibres interspersed in a thin layer of connective tissue. Sphincters of a moderate size are situated immediately proximal to the two lips.

Pigment cells (fig. 45) of a yellow colour are found scattered among the epithelial cells as well as in the connective tissue. There is, however, a greater concentration of pigment cells in the connective tissue of the lips, so that the area covered by these lips is of a brown colour and can be easily distinguished from the surrounding tissue.

(d) *Sinuses*. The sinuses lie in the loose connective tissue of the nephridia, the separating wall between the lumen of the nephridium and a sinus being so thin that the fluid waste products are continually drained off from the sinuses into the nephridium by the action of the excretory cells. In some cases, the sinuses contain scattered corpuscles as well as shapeless cells which migrate from the nephridium.

(e) The *pericardial glands*. The pericardial glands consist of scattered glandular cells interspersed with pigment cells. Although the gland cells are chiefly confined to the distal portions of the auricles, they are also found in small numbers among the epithelial cells of the pericardium. These pigment-cells (fig. 30 c) give a peculiar brown colour to the auricles.

The glandular cells are found in the loose connective tissue beneath the single-celled epithelium of the auricles. Each glandular cell is more or less oval in shape, full of protoplasm with a distinct nucleus in the centre. Such cells are found in comparatively large numbers in the area opposite the funnel of the reno-pericardial canal. The pigment cells contain a cryatalline yellow pigment and are found scattered irregularly among the glandular elements. The glandular as well as pigment cells of the epithelium of the pericardium, however, are more or less cubical, like the rest of the epithelial cells.

THE REPRODUCTIVE ORGANS

Ostrea cucullata is normally dioecious but hermaphrodite forms are also occasionally met with. In a collection of 794 specimens, the proportions of the different forms were:

Sex	Numbers	Percentage
Male	326	41.7
Female	445	56.4
Hermaphrodite	23	2.9
	794	100

In a young oyster, the gonads consist of a pair of branching tubular glands. As the oyster attains maturity, the gonads increase in size and the branches of the two sides come together and coalesce, forming a network which extends over the whole of the visceral mass during the breeding season. The gonads when viewed under a lens at this stage present an elaborate arborescent structure (fig. 4).

The genital products leave the gonads through ciliated genital tubules and pass out to the exterior through two gonidial apertures (fig. 43) situated in the reno-gonidial grooves dorsal to the renal apertures on either side of the pylorus. The two apertures indicate the paired origin of the gonads during development. The epithelial cells of the vestibule (reno-gonidial groove) are strongly ciliated and aid in conveying the renal and genital products to the exterior.

It should be noted that in *Pecten* and *Placuna placenta*, the genital products are emitted into the renal organs, but in *Ostrea cucullata* and *O. edulis* the genital ducts are quite independent of the renal ducts, and merely open into the common reno-gonidial groove, from which the genital products are carried to the supra-branchial chamber on their way to the exterior.

Fig. 46 A is a section through the male gonad. It consists of densely packed spermatozoa, which stain so deeply that the outline of the germinal epithelium proper is difficult to distinguish. Compared to the ova, the mature spermatozoa are extremely minute, consisting of a rounded head which stains deeply and a long protoplasmic tail, about ten times the length of the head (fig. 46 B).

Fig. 47 A shows a female gonad. The cavity of the stroma is filled with ova in various stages of development, which are

budded off from the germinal epithelium. A mature ovum of the oyster (fig. 47 C) is a large spherical structure about $46\ \mu$ in diameter, with a large rounded nucleus and a distinct nucleolus.

Fig. 48 is a section through a hermaphrodite gonad, showing the ova and spermatozoa in the same follicle. This shows that the male and female elements really take their

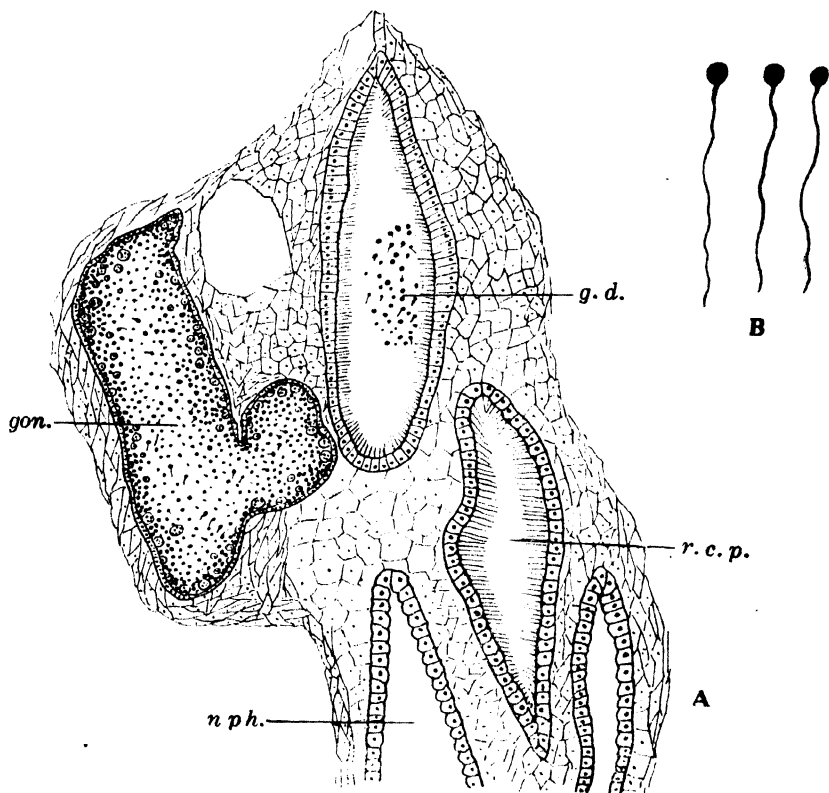


Fig. 46.—A. A section passing through the ripe male gonad, the gonidial duct and the reno-pericardial canal. ($\times$ cir. 300). B., Sperms highly magnified. ($\times$ cir. 900). *g. d.*, gonidial duct; *gon.*, male gonad (testis); *nph.*, nephridium; *r. c. p.*, reno-pericardial canal.

origin from the same germinal epithelium. When the gonads of a large number of fresh hermaphrodite individuals are examined under the microscope, the eggs and sperms are found to be identically similar to those of diœcious individuals but are never found in equal proportions.

Amemiya¹ suggested that all oysters can be divided into dioecious and monœcious forms, which can be distinguished in the following manner: "The eggs of the monœcious forms are relatively large (about 0.1 mm. in diameter), the ova are fertilized in the shell cavity of the mother, the zygote remaining therein while passing through the 'white sick' and 'black sick' stages of the metamorphosis, and it is only when the young have themselves become equipped with well-developed shells that they pass into open water to begin their independent existence. In the dioecious forms,

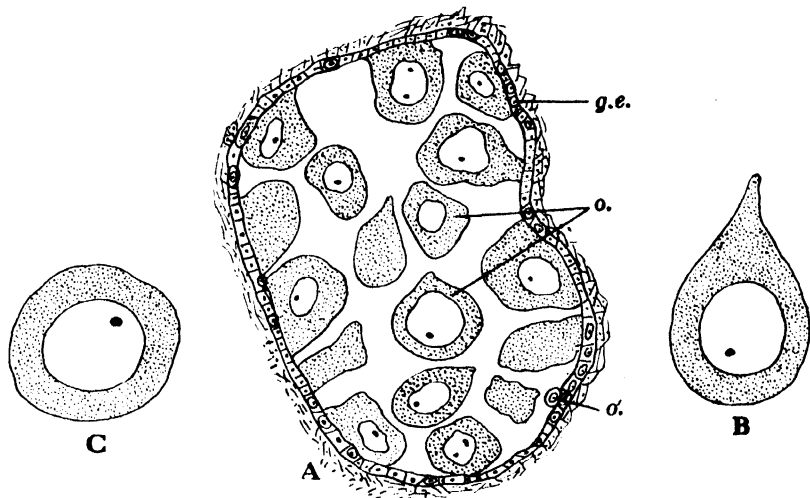


Fig. 47.—A., A section of the right ovary showing the germinal epithelium and the developing ova. B., Unripe ovum. C., Nearly ripe ovum. *g. e.*, germinal epithelium; *o.*, ova; *o¹.*, ovum cell just budded off from the germinal epithelium. ($\times$ cir. 300)

on the other hand, the ova are smaller in size; the gonads of sexually mature individuals are shed into water; fertilisation occurs in the open sea and the resulting zygotes pursue their development independently from the very beginning." According to this definition, *O. cucullata* is normally dioecious since the ova are small and development takes place outside the shell in the open sea.

It is interesting to note that the pea-crab (*Pinnotheres*) found within the shells of *O. cucullata* exerts a profound

1. Amemiya, Ikusku.—"Hermaphroditism of the Portuguese oyster", Roy Phy. Soc., Vol 21, Pt. 2, 1926.

influence on the sex of this oyster so that the majority of oysters thus inhabited are either males or hermaphrodites—the number of females being extremely small. Figures showing the proportion of sexes in the oysters harbouring the pea-crab have already been given on page 12. These figures show that the pea-crab has something to do with the change of sex, either by reducing the food supply of the

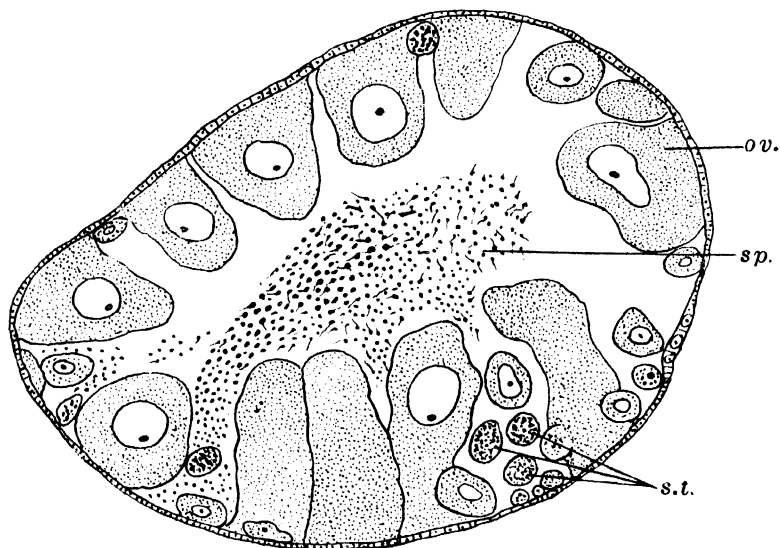


Fig. 48.—A section through the hermaphrodite gland. *ov.*, ovum, *sp.*, sperms; *s. t.*, spermatie cells. ($\times$ cir. 650)

oyster or by bringing about a change in its general metabolism. Moreover, it has been observed that hermaphrodite individuals appear chiefly during the monsoon, so that hermaphroditism in this case may be due to deficient food-supply and unhealthy conditions of that season. Hermaphroditism is very rare at other times of the year.

Orton¹ has recently made some very interesting observations on the change of sex in *Ostrea edulis*. He has

1. Orton, J. H.—“Observations and experiments on sex-change in the European oyster (*O. edulis*). Pt. I. The change from female to male.” Journ. Mar. Biol. Assoc., Vol. 14, 1927.

—“A note on the physiology of sex and sex determination,” Journ. Mar. Biol. Assoc., Vol. 14, 1927.

suggested that "sex-change is due to a metabolic rhythm in two phases; there is some evidence—as yet, however, incomplete—that in one phase protein metabolism is prominent and is accompanied by egg development; while in the other, carbohydrate—and especially glycogen—metabolism is predominant, and is accompanied by development of sperms." Brambell¹ is of opinion that "the chief environmental factors likely to operate would lie in the nature of nutrition or of hormone action."

Some of the experiments made by the authors themselves are also instructive. Holes were drilled into different oysters and their sex determined by examining the contents of the gonads under the microscope. The female specimens were left in the laboratory tank and were examined at regular intervals. After a week it was found that there was a change of sex from female to hermaphrodite and finally to male. There being practically no food in the tank, the obvious inference was that the supply of food determined the sex.

1. Brambell, F. W. R.—"Sex-reversal and intersexuality", *Journ. Roy. Micr. Soc.*, xxiv, 1923.

THE DEVELOPMENT

1. *The Spawning Season.*

In order to determine the spawning season of *O. cucullata*, tiles were placed on oyster beds (Mahim and Santa Cruz¹) to catch the spat. These were examined at regular intervals not exceeding a fortnight. In addition, the condition of oyster beds in other places was also observed in different seasons.

These observations have shown that along the coast of Bombay, spawning continues almost throughout the year except during the monsoon—from the middle of June to about the end of September. During the monsoon, there is a sudden change in the density of sea-water which may fall below 1.012. This affects the metabolism of the oyster and causes a great deal of mortality amongst them. The spawning period starts about the middle of October, when the average temperature of the land is about 83.7°F. and the density of the sea-water is 1.021. It continues throughout the winter months but owing to the low density of sea water during these months, the spawning is not so regular or prolific. The principal season seems to start during the month of March and is indicated by a heavy spat formation. The heaviest spatting seems to occur during the hot months of April and May and continues throughout June, if there is no marked change in the weather. In June the land temperature is usually at its highest and is always about 87°F.

We can thus distinguish a *regular season* (March to mid-June) in which there is a heavy spat-formation and an *irregular season* (October to February) when the spat-formation is small and irregular. This is in marked contrast with the condition in the European oyster (*Ostrea edulis*), in which the spawning season is strictly limited to the summer months—the largest proportion of mature females occurring at the beginning of summer and gradually diminishing as the summer advances—so that at the end of the breeding season only a few females with ripe ova remain.

1. These are the two principal places with oyster beds round the Island of Bombay.

Salinity and temperature of sea-water seem to be the two chief factors controlling the spawning of the oyster. The optimum salinity for the spawning of *O. cucullata* seems to be in the proportion of 3: 1 of brine and fresh water and the optimum temperature from 80° to 87°F.

2. *Fertilisation and Segmentation.*

The development of *O. cucullata* was studied by artificial fertilisation of the eggs. The results thus obtained were quite satisfactory, since almost 100% of the eggs were found to develop under artificial conditions. The initial developmental stages were successful only when the temperature and the salinity of the water were suitable.

At a fairly high temperature (82°—85°F.), segmentation starts early and development proceeds satisfactorily, but if the temperature falls below 78°F., development slows down, the embryos and larvae become inert and finally succumb completely. Another important factor that affects the development of *O. cucullata* to a large extent is the degree of salinity of sea-water. Culture media of various strengths were prepared for this purpose by mixing sea-water with fresh water and the effects of the different mixtures on development were recorded. The mixture that gave the best results for this species was found to be of about 1.020 or 1.021 density, the proportion being about three parts of sea-water to one part of fresh water.

Just before starting the fertilisation experiments, mature sperms and eggs were taken out and placed in separate dishes in sea-water for 20 to 30 minutes. The contents of the two dishes were then mixed and the results observed. Almost immediately, the active sperms crowded round the eggs and one of the sperms entered each egg-membrane and fertilised the ovum.

Two types of eggs are met with, the spherical (fig. 47C) which are nearly ripe and ready for fertilisation, and the oval or flask-shaped (fig. 47B) which are unripe and cannot be fertilised. These latter have a rounded body and a tapering end by which they are attached to the germinal epithelium. The gelatinous envelope which covers the eggs of other Lamellibranchs seems to be absent in this type. The nucleus is comparatively large and very clear and seems to

disappear from view soon after fertilisation. Owing to this phenomenon, the number of eggs which are fertilised and are capable of development can be easily reckoned. The immature eggs incapable of fertilisation can also be distinguished from the rest by their amoeboid movement in sea water.

The following is a table of developmental stages under favourable conditions—the optimum temperature being 82°—85° F. and the density of the sea-water 1.020:

- | | | | |
|----|---|---|-----|
| 1. | 1st Polar body..... | 35-40 minutes after the mixing of the sperms with the eggs. | |
| 2. | 2nd ,, ,, ... | 40-45 ,, | do. |
| 3. | First segmentation division | 50-55 ,, | do. |
| 4. | Morula stage just before the rotating embryo .. | 3½ hours | do. |
| 5. | Rotating stage | 3½ ,, | do. |
| 6. | Invagination and the gastrula stage..... | 7-9 hours | do. |
| 7. | Trochophore stage | 20 ,, | do. |
| 8. | Veliger larva | 48 ,, | do. |

The first visible change after the disappearance of the nucleus is the extrusion of polar bodies towards the broader end of the oosperm. The first polar body is given off after 35-40 minutes and the second immediately after the first. The first polar body is a small transparent knot, which projects from the edge of the ovum and remains in contact with it for a considerable period in most cases (fig. 49).

About 50-55 minutes after fertilisation, a dent appears at the narrow end of the oosperm opposite the point from which the polar bodies are thrown off. Rapid rotating movements of the protoplasm occur and are soon followed by another dent near the point of extrusion of the polar bodies. In this way the zygote is divided into two unequal cells. The small cell or micromere soon divides and sub-divides until a layer of small cells is formed, which ultimately forms an outer layer enclosing the large cell (fig. 49).

The large cell or macromere divides forming an inner layer, which becomes the lining of the embryonic gut. Finally, the micromeres become ciliated and completely surround the macromeres except at one point, where the continuity is broken by the presence of the blastopore.

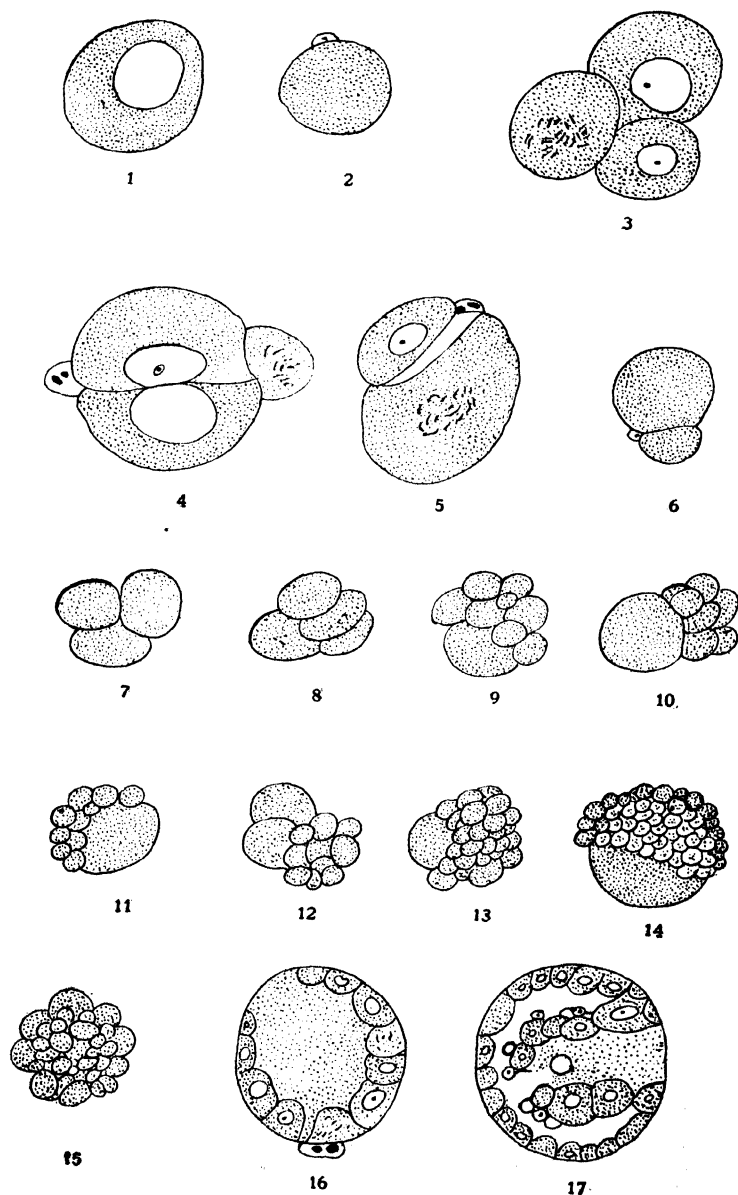


Fig. 49.— Early stages in the development of *Ostrea cucullata*. 1. Unfertilised egg. 2. Fertilised egg with a polar body (about 40 minutes after

3. The Formation of the Gastrula.

Gastrulation is brought about by two processes—*epiboly* and *invagination*. The characteristic shape of the larva becomes transformed into a flattened disc, and a shallow depression appears which grows deeper until the edges almost meet and fuse to form the digestive cavity. At this stage the larva is almost spherical in shape and swims about rapidly by means of its cilia (fig. 50).

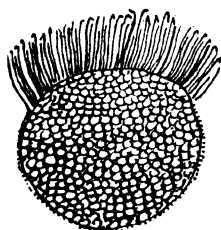


Fig. 50—Trochophore larva
18 hours old. ($\times 400$)

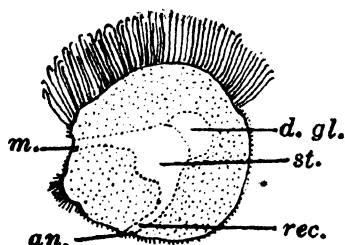


Fig. 51—Veliger larva nearly two days
old. *an.*, anus; *d. gl.*, digestive gland;
m., mouth; *rec.*, rectum; *st.*, stomach.
($\times 400$)

4. The Veliger Larva.

Very early in development, the ectoderm becomes differentiated giving rise to various structures. The prostomial region grows into a thickened rim bearing the pre-oral circlet of cilia, and called the *velum*: the larva at this stage is distinguished as a *veliger*—a very characteristic stage in molluscan development. The velum is the chief organ of locomotion at this stage and appears when the larva is about 18-20 hours old. Further, there is an invagination of the dorsal surface of the ectoderm which gives rise to the *shell-gland* and extends downwards to cover the entire surface of the body except the velum.

fertilisation.) 3. Pseudo-three-celled stage (50 minutes after fertilisation). 4 Two-celled stage (Two cells of the preceding stage ready to fuse). 5. Section of the two-celled stage showing the segmentation cavity 6. The egg in the two-celled stage, one hour old. 7. The three-celled stage, with one large and two small cells. 8. Four-celled stage. 9. Embryo of about $1\frac{1}{2}$ hours. 10. Another view of the same. 11—14. Different stages in the development, showing one megamere capped over by a large number of micromeres. 15 Embryo of about $2\frac{1}{2}$ hours, viewed from the upper pole. 16 A section of a morula about 3 hours old. 17. A section of the gastrula about 7 hours old. (Figs. 4, 5, 16 and 17 $\times$ cir. 675; all others $\times$ cir. 300.)

The ectoderm of the veliger larva (fig. 51) is ciliated all over but bears extremely long and thick cilia on the velum in front of the mouth. This pre-oral ring of cilia is characteristic of the trochophore larvae of both Annelids and Molluscs and is therefore of phylogenetic interest. By means of their cilia, the larvae at this stage swim very actively in all directions and crowd near the surface of the water.

Fig. 51 represents a veliger larva drawn from life, showing the long cilia of the velum and the smaller cilia around the base. The mouth is visible behind the velum and leads into the oesophagus, which in its turn opens into the stomach; the stomach is followed by a small gut and the rectum, which opens to the exterior through the anus. The vestigial foot lies between the mouth and the anus but is quite small and functionless.

THE OYSTER FISHERY

“There is abundant evidence that marine molluscs were extensively used for food by man before historic times. In many parts of the world, ancient shell heaps, some of them of immense proportions, are found near waters that are still capable of producing the same forms. These are so disposed and so constructed that it is certain that they are not natural accumulations on what was formerly ocean bottom, but the work of human hands. This conclusion is substantiated by the fact that among the shells of clams or oysters or marine snails, the bones of aquatic and land animals are often found, together with primitive weapons or domestic implements.” (Kellogg¹).

There is no doubt that the molluscs as a class have been used as food by man throughout the ages. Owing to prolific reproduction and rapid growth, they occur in abundance in many localities. All molluscs store large quantities of animal starch or glycogen and fat which make them highly nutritious as food². But the oyster of all the shell-fish has made the greatest appeal to the human palate and has formed a favourite food with many people. The ancient Romans consumed enormous numbers of oysters in their sumptuous banquets. A Roman emperor, Aulus Vitellius, whose feats of gluttony have probably never been surpassed before or since, is said to have eaten a hundred dozen oysters at a single meal³. It is no wonder then that the Romans were the first to develop the oyster industry by artificially replenishing the natural oyster beds. These methods of oyster culture started by the Romans are still used in Lake Fusaro in the south of Italy. At the present day, oyster culture forms an important industry in France, the United States and Japan, and attempts are being made in other countries as well to develop this industry. In France, the home of oyster culture, many thousands of people are engaged in the industry. Out of the three main centres, Archachon alone (situated some fifty miles south of Bordeaux) with its extensive beds exports 300 to 500 million

1. Kellogg, J. E.—“The shell-fish industries,” New York, 1910.

2. Yonge, C. M.—“Queer Fish,” London, 1928.

3. Roughley, T. C.—“The Story of the Oyster,” Sydney, 1925.

oysters every year. In fact, "the whole industry in both its history and modern developments forms an object lesson in the value of applied Biology."

In India, oysters have been used as food for many centuries, but the methods employed for extracting and rearing oysters are crude even to-day. Recently, however, the Fisheries Department at Madras have made a small beginning in using scientific methods for oyster culture.

In the vicinity of Bombay and along the coast of the Presidency, most fishermen collect oysters from their natural beds which are easily accessible, and sell them immediately in the nearest market either as "shelled" or as "shucked" oysters. In "shucking", the edges of the shells are broken and the adductors cut by inserting a blade of knife within the shell. The meats are then removed or "shucked" and put away in a vessel containing sea water, until they are sold as oyster "meats." This process of shucking is generally done near the beds and the shells are thrown back into the sea. Ordinary fishermen take no pains to make the oysters presentable in the market; but live from hand to mouth and sell their stock from day to day.

A few fishermen, however, invest some money in the oyster industry and employ labour for picking oysters from their natural beds and planting them on suitable hard grounds near low tide-water mark. If the ground is naturally soft, it is hardened artificially with sand, clay and shells. Oysters thus planted are looked after very carefully for two or three years until they are ready for the market. During this time the oysters are cleaned by turning them over, and the grounds changed if it is found that there is a great deal of mud and slime deposited on the oysters. The growth of the oysters under these improved conditions is very rapid, the average size of a marketable oyster being about 8.5×8.5 cm. The price realised is very low, ranging from six to twelve annas per dozen, but fishermen who own planted beds, can afford to wait and sell them at higher prices. It is said that these fishermen supply from 2,000 to 3,000 dozen of oysters per month to hotels and clubs in the city as well as in mofussil stations and make an average yearly income of three to five thousand rupees. It is very difficult, however, to get any exact data of the sale from these men.

The implements used for picking oysters are not at all expensive: a hand-dredge consisting of a net attached to a triangular frame made of bamboo with a handle of the same material, a spade, a pick-axe and a knife with large blades being the main tools a fisherman employs in plying his oyster trade. He never works in waters deeper than three to four feet.

As a rule, there is no limit to the number of men that are employed in picking oysters and the beds are not closed for fishing even in the spawning season. The idea seems to be that natural beds are inexhaustible. But in certain estuaries near Karachi, men with a Government license alone can pick the oysters and that in the open season so that some beds are closed for fishing for longer or shorter periods.

The Bombay oysters are used as food by the public chiefly in the winter months *i. e.* from November to March. During the monsoon, the oysters seem to lose their flavour, their meats becoming watery owing to a large influx of fresh water. They are then not wholesome as food. In the months of April, May and June, the public eschew them, since they are supposed to carry typhoid bacilli, although they are then in the best condition of their life, with the visceral mass full of gonidial tissue.

Broken shells are extensively used for making lime, so that the fishermen are able to make some money by selling the broken shells to building contractors at a very cheap rate of four to six annas a maund.

DIRECTIONS FOR PRACTICAL WORK

Oysters for purposes of dissection can be obtained from their beds by scraping them with large knives. It is best to bring them in sea-water to the laboratory so that they can be examined in a living condition. As far as possible, large sized oysters should be selected, as they are more suitable for dissection.

In order to observe the inhalent and exhalent currents of water, fine particles of carmine should be sprinkled on the surface of sea-water containing the oysters. Carmine particles can then be seen travelling inwards with the inhalent current (ventro-posterior region) and coming out with the exhalent current (dorso-posterior region) as shown in fig. 5. Similarly, after removal of a part of the right mantle, the direction of currents on the mantle, the gills and the labial palps can be observed.

Animals for dissection should be narcotised by the following method recommended by Dakin:

To 200 c.c. of sea-water, add 100 c.c. of glycerine and 100 c.c. of absolute alcohol. This mixture should be gradually added to the sea-water containing the animal. After about 24 hours or sometimes less, the animal is completely anæsthetised in a fully extended condition. It can then be transferred to a fixative for section-cutting or other purposes.

1. *The shell.* Before dissecting the animal, make a note of the colour, size and shape of the shell as well as the lines of growth of the shell. The orientation of the animal should be clearly grasped, *i.e.*, the anterior and posterior ends, the dorsal and ventral edges and the right and left sides.

In an empty shell, note the right and left valves fitting closely into each other and forming a water-tight compartment when closed. Note also the ridges and folds at the margins of the shell-valves specially on the left valve (figs. 2 and 3).

Note the smooth and polished inner surfaces of the valves as well as the shape and colour of the muscle-scar. The pallial muscle-scars lie within a short distance from the margin of the valves. The hinge-area is straight and toothless. Observe the denticles in the right valve and the corresponding grooves on the left.

2. *General Dissection.* In order to expose the soft parts of the animal for dissection, remove the right valve by passing the blade of a knife through the hinge-area and cut the elastic ligament and the adductor muscle lower down. Care should be taken not to insert the knife along the dorsal or ventral margin, as this may injure the soft parts of the animal lying in the hollow of the cup-shaped left valve. On removal of the right valve, the right mantle-lobe will be found to envelop the soft parts of the entire animal. Before removing this mantle-lobe, the following structures should be identified:

- (1) Attachment of the mantle with the surface of the body and the gills.
- (2) Union of the mantle-margins with each other forming the so-called "sutures"; the thickness of the margin, the arrangement of tentacles and the distribution of pigment on the margin.
- (3) The distribution of pallial sinuses and nerves.
- (4) The pallial cavity between the right and left mantle-lobes.

3. *General Anatomy.* Cut the right mantle-lobe along its place of attachment with the gills and the sides of the body, and identify the following structures (figs. 4 and 5):

- (1) The adductor muscle.
- (2) The gills.
- (3) The pericardium.
- (4) The labial palps.
- (5) The visceral mass beneath the gonads.
- (6) The pyloric cæcum.
- (7) The renal organs (nephridia) and the reno-gonidial aperture.
- (8) The rectum and the anus.
- (9) The pallial sense-organ attached to the ventral side of the adductor muscle.
- (10) The visceral ganglia.

Note that the cephalic region is vestigial; there is no distinct head; and that the foot and the siphons are absent.

4. *Gills.* Make a transverse section of the gills and note the W-form of the cut ends; the arrangement of blood-vessels along the gill-axis; the inter-filamentar and inter-lamellar junctions; the water-pores opening into the supra-branchial chamber; and the deep groove at the margin of the gill (figs. 8, 10 and 15).

Microtome sections of the gills at different levels (figs. 9 to 16) should be examined for the following:

- (a) The formation of a plica.
- (b) The principal, transitional and ordinary filaments.
- (c) The blood-vessels and muscle-fibres.
- (d) The size of each filament and the position of its cilia and chitinous rods.

5. *The adductor muscle.* Note the shape and size of the muscle and its division into two regions. Muscle-fibres should be teased out, mounted in glycerine and examined under the microscope.

6. *The heart and the blood-vessels.* Cut open the pericardium lying anterior to the adductor muscle and remove the pericardial wall. The following structures will then be visible:

- (a) The ventricle with its thick muscular walls.
- (b) A pair of auricles with thin pigmented walls.

Count the number of heart-beats per minute in a live specimen.

In order to study the blood-vessels, borax-carmin in 70% alcohol should be injected through the ventricle of a living animal by means of a fine capillary pipette. By a regular continuous pressure, arteries can be injected successfully in this way. Veins should be injected through the common afferent vein and the efferent vessels through the branchial efferent. The injected specimens should be dehydrated, cleared first in cedar oil and later in oil of winter green. Specimens should then be dissected out under a binocular dissecting microscope for different vessels.

7. *The excretory organs.* Note the external reno-gonidial aperture near the anterior bend of the adductor muscle. The nephridia lie on the dorsal side of the pyloric cæcum between the pericardium and the crystalline style sac. The whole course of the right nephridium can be easily demonstrated by injecting borax-carmin in 70% alcohol through the reno-gonidial aperture. Note the following structures in the nephridia (figs. 40 to 43).

- (a) The anterior course of the nephridium.
- (b) The inter-nephridial canal or passage.
- (c) The posterior course of the nephridium.
- (d) The reno-pericardial canal. (This can be demonstrated by inserting a fine bristle into

the pericardial opening and drawing it out through the nephridial opening).

8. *The alimentary canal.* The greater part of the alimentary canal lies embedded in the visceral mass. A seeker should be inserted through the mouth into the œsophagus and the latter slit open. On removing the gonidial tissue with a pair of needles, the dark brown digestive glands can be seen surrounding the stomach on all sides. The stomach should be opened and the following points noted:

- (a) Deep grooves and ridges on its internal walls.
- (b) Openings of the ducts of digestive glands.
- (c) The gastric shield lying on the left wall of the stomach.
- (d) The crystalline style-sac. In a fresh specimen, the style will be almost transparent and solid, filling the cavity of the sac; but within half an hour or so of the removal of the animal from sea-water, the style will dissolve and disappear.

Slit open the intestine along its whole length by using a seeker as a guide and note the single loop it forms on the left side of the body. Follow up the typhlosole in the intestine and the rectum.

In order to study the contour of the inner wall of the stomach, a mixture of melted paraffin, gelatine and carmine or gelatine and carmine without the paraffin should be injected into the stomach through the œsophagus. Injected specimens should then be placed in 5% formalin. When the mixture solidifies, a good cast of the stomach is formed, which can be removed by a careful dissection.

9. *The nervous system.* It is difficult to dissect out the whole course of the nervous system. It should be studied as thoroughly as possible from microtome sections.

The right cerebral ganglion can be dissected out by pressing aside the lower edge of the outer labial palp. The left one lies deeply embedded in the connective tissue between the digestive glandular tubules. The cerebro-visceral connectives are also buried in the connective tissue and are therefore difficult to be traced in dissections. The visceral ganglia and the nerves arising from them can be easily dissected and exposed to view if the gills are pushed aside.

10. *The reproductive organs (gonidia).* The sexes are separate and there are no external distinguishing characters

between the male and the female. The gonads, when ripe, cover the whole of the visceral mass. The gonidial ducts can be easily demonstrated by injecting borax-carmine through the reno-gonidial aperture. The gonidial duct opens into the common vestibule just on the dorsal side of the nephridial opening.

Examine a few eggs and sperms obtained by teasing a small portion of the gonads in salt solution.

11. *The development.* The early stages of development can be studied by artificially fertilising the eggs. For successful fertilisation, sperms and eggs should be taken from mature individuals and kept in sea-water in separate sterilised dishes for about 15 to 20 minutes. A pipetteful of spermiatic fluid should afterwards be mixed with the fluid containing the eggs. The latter, if mature, will immediately be fertilised, the evidence of which will be the rapid segmentation of the egg followed by a gradual development of the larva.

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